EXD. R

Vol. 91. Part 10. Pp. 459–557, 24 figs., 1 map. 1st December, 1941

THE

TRANSACTIONS

OF THE

ROYAL ENTOMOLOGICAL SOCIETY

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LONDON:
PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price £1 10s. 0d.

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THE TAXONOMY AND ECOLOGY OF THE NYMPHS OF BRITISH PLECOPTERA WITH NOTES ON THE ADULTS AND EGGS

By H. B. N. Hynes, Ph.D., A.R.C.S., F.R.E.S.

With Twenty-four Text-figures.

Manuscript received 28th November, 1940.

(Read 4th June, 1941.)

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I. Introduction.

This paper represents the greater part of a Thesis approved by the University of London for the degree of Ph.D.

Stoneflies, particularly in their nymphal stages, form an important part of the food of such fish as trout and young salmon, and, in almost all aquatic habitats which have well-aerated water and a stony substratum, the nymphs are numerous and form a large and important part of the fauna. Little, however, is known about their ecology, and in this country particularly workers who have dealt with the group have confined themselves almost entirely to the taxonomy of the adults. Among European workers Schoenemund (1924) and

Kühtreiber (1934) have described the habitats of the nymphs of several species, but neither has made any attempt to explain the factors controlling their distribution. It is probable that the difficulty of identifying the nymphs has been the chief reason why so little work has been done on their ecology, but in Britain, where there are comparatively few species, investigation presents fewer difficulties.

The present investigations, which were made over a period of two years, were undertaken with the primary object of ascertaining the factors controlling the distribution of the various species, but, before this could be done, means had to be found of identifying stoneflies in all stages of development. Accordingly, the whole of the spring and summer of the first year had to be devoted to the rearing of nymphs to maturity, and to working out the taxonomy of the nymphs in all stages. This, and all later work, was done at the Wray Castle Laboratory of the Freshwater Biological Association of the British Empire, in the English Lake District. A map showing that part of the Lake District in which most of the collections were made is given at the end of the paper. Material was, however, obtained from other parts of the country, and was found to agree largely with observations made within the Lake District. The second year was devoted to an intensive study of the ecology of the group within the Lake District. The geology of this district is very uniform, so it was possible to compare many similar localities one with another, and to find whether observations made in one locality agreed with those made in similar localities many miles away. This uniformity of geology has, however, the disadvantage that any gross chemical factors, which might be supposed to affect stoneflies, could not be investigated, because of the chemical similarity of most bodies of water within the Lake District. The fact that such factors do influence the stonefly fauna has been indicated by Miss Frost's work on the River Liffey. Observations made in Scotland and southern England suggest, however, that many species occur in any bodies of water that are physiographically suitable.

The classification of the nymphs has been given here in considerable detail because it is hoped that it will be of use to ecologists investigating more general aspects of the ecology of fresh water, and because it is the first attempt to find means of separating the early stages of stoneflies in this country.

In the section on ecology the habitats of each species are described, and possible explanations for the distribution of the species in the various types of habitat are advanced. The chief difficulty encountered in this section of the work has been the lack of any recognised system of classification of bodies of fresh water. A system has, however, been evolved with special reference to stoneflies, and it is possible that this, with certain modifications, could be used in studies on the ecology of similar groups of aquatic insects, such as the Ephemeroptera and Trichoptera.

I wish here to acknowledge the help given to me during the course of this work. I am particularly indebted to Dr. E. B. Worthington, who supervised my work, gave me much helpful advice, and placed at my disposal the resources of the Wray Castle Laboratory and staff of the Freshwater Biological Association of the British Empire, and to Mr. D. E. Kimmins, who helped with the identification of the adults, and the somewhat involved nomenclature of the group. Dr. T. T. Macan and Dr. J. W. Jones have both made collections for me in Hampshire, and Dr. Macan has offered much helpful advice and criticism throughout the course of the work. Dr. Dorothy Hill has helped me considerably with the classification of the nymphs of the difficult genus *Leuctra*, and Dr. Marie Rosenberg and Miss W. Pennington were of great assistance in the

identification of algae eaten by the nymphs. Mr. H. J. Buchanan-Wollaston has helped me with the statistical presentation of the data on the length of life and growth rate of the nymphs, and Miss W. E. Frost has kindly allowed me to use her figures on the growth rate of *Protonemura meyeri* obtained during her work on the River Liffey in Ireland. I am also indebted to several people, and in particular to Miss Frost, for enabling me to examine material collected in other parts of Britain. I am grateful also to the Department of Scientific and Industrial Research, which granted me a maintenance allowance and so enabled me to carry out this work.

II. Methods and Technique.

The nymphs were collected with a stout pond net, or by sorting over vegetable matter removed from the water by hand. On stony substrata the method used was to kick up the bottom with the feet and to scoop up the resulting cloud of detritus and other light matter with the net. By this method all the unattached animals present were caught in the net, the contents of which were then sorted over in a dish of water. When the nymphs were very small, the contents of the net were taken back to the laboratory and sorted there. Nymphs living in the moss on the tops of stones, or in packets of dead leaves, were obtained by hand-picking the moss or leaf packets, which were taken back to the laboratory for sorting. Species living in the submerged parts of emergent vegetation or in rooted aquatic vegetation were obtained by scooping up the vegetation with the net, and sorting it over in a dish of water.

The adults were collected by means of a sucking-tube, a net being unnecessary because they did not attempt to fly when disturbed. They were usually found on the undersides of stones on the bank.

In order to find means of identifying the nymphs it was necessary to rear every species to maturity in captivity, and so to correlate the nymphs with their respective adults. It was found that most species would not live in still water in the laboratory, but would live well in running tap water. Accordingly an artificial stream was constructed in which there were sixty separate compartments. It consisted of a series of six steps sloping at 15 degrees, each step being wide enough to take ten flat enamel pie-dishes. The pie-dishes were 9 inches by 11½ in. and 2 in. deep, and each was covered with mosquito netting or bolting silk sewn on to a wire frame; the frame was slightly larger than the dish, and was held on to its edge by four wire paper clips. There were thus ten series of six sloping dishes, the bottom end of each dish being over the middle of the one below as illustrated in the accompanying diagram. Tap water was dripped by a series of glass and rubber tubes on which were screw clips, through the netting on each top dish, and it flowed over from dish to dish. The water from each of the bottom dishes was collected in a trough and flowed away to waste. Each dish, therefore, had running water, but nymphs could not get from one dish to another because of the netting, and adults when they emerged were confined in the space below the netting in the upper part of the dish. Several stones were placed in each dish for the animals to cling to, and the appropriate food for the species was added also. The whole apparatus was kept in the basement at Wray Castle, where the temperature is normally about 14° C., and varies little throughout the year. All species, except *Brachyptera risi*, lived well under these conditions. The reason for the failure to keep *B. risi* alive may have been the presence of iron in the tap water, but the species is very delicate, and specimens were often dead or dying when brought back to

the laboratory. It was necessary, therefore, to rear this species in breeding cages in the field. These were boxes made of non-corroding metal, of which two sides were replaced by metal gauze, placed in the stream from which the nymphs were collected, so that there was enough space in the box above water for emergence of the adult. Nymphs from still water were reared in dishes similar to those used on the artificial stream, but through which water was not running. While the work of rearing was in progress each dish or breeding cage was inspected every day, and the adults and their cast nymphal skins removed. In this way large numbers of nymphs from many localities were reared to maturity, and sufficient material was obtained to allow the taxonomy of the nymphs to be worked out.

Eggs were also hatched in the artificial stream, by placing each egg mass in a small tube closed at both ends with bolting silk, and putting the tubes in one of the dishes. Some species, notably the PERLODIDAE, would not hatch under these conditions, and it was later found that those species which would hatch there hatched equally well in shallow still water in small glass containers.

During the first year of the investigation, some specimens of each collection made were preserved, and some were reared to maturity. In this way a collection of nymphs of known species was amassed, and it is on this collection that the classification of the nymphs has been worked out. Later the same localities were revisited, and the young stages were obtained, and identification of these was confirmed by watching development in the field, and making confirmatory collections of adults.

In the course of this work the stonefly fauna of several frequently visited localities was worked out, and it is on this data that much of the ecology was obtained. At the same time collections were made in many other localities in the Lake District for purposes of comparison, and collections were made in Hampshire, Surrey and Caithness. Localities in Nottingham and Suffolk, from which the species *Isoperla griseipennis* and *Nemoura dubitans* respectively have been recorded, were visited, but neither species was found.

Two per cent. formaldehyde was used to preserve all the stoneflies and nymphs. The adults were first wetted in 70% alcohol and then placed in the formalin, and the nymphs were placed directly in the preservative. Formalin was found to have advantages over alcohol as a preserving medium, in that it does not dry up so readily, keeps the colour of the specimens much better, and does not render them so brittle.

The nymphs were described from newly preserved material under a low power prismatic binocular microscope, and permanent balsam mounts were made of mouth-parts and similar structures, on which more detailed observations were necessary. The nymphs were first broken across at some convenient place and boiled for some minutes in 20% caustic potash to remove the soft parts. Dissections were then made in 70% alcohol, after washing in water, and the parts to be mounted were transferred to a saturated solution of phenol in absolute alcohol. They were given two washes in this and then transferred to balsam. In the small species it was found helpful to stain the mouth-parts in carbol-fuchsin; they were then taken up to absolute alcohol and through xylol to balsam in the normal manner. In studying the arrangement of the bristles in the genus *Leuctra* and in small specimens of *Protonemura*, it was found helpful to boil the specimens in 20% caustic potash and then to examine them in alcohol by transmitted light, with a high-power monocular microscope. This was preferable to making balsam mounts, because the bristles remained in their natural positions.

For the purpose of investigating feeding habits, specimens in as many stages of development, and from as many localities as possible, were examined for gut contents. The methods employed are described in the section on feeding habits.

The growth rates of several common species were also investigated. Localities where each of the species was known to be common were visited at approximately monthly intervals throughout the period of the year during which the nymphs could be found. As many specimens as possible were collected, care being taken to find every specimen caught in the net or in the moss or leaf-packets, and each was then killed in 2% formalin and measured against squared paper.

The figures of the nymphs and the eggs were drawn by three different methods, and these have been indicated by the small letters in brackets in the legends. Those marked (s) were drawn from preserved material under a low power prismatic binocular microscope, with the aid of a squared eye-piece. Those marked (m) were drawn under similar conditions, but without the squared eyepiece, the proportions being based on measurements. Those marked (cl) were drawn with the aid of a camera lucida on a high-power monocular microscope; all drawings made in this way, with the exception of figs. 10J, 14N and 14O, 17 and 24, were drawn from balsam mounts. On several figures a number of scales have been used, and these have been given in the figure. The number in Roman figures in brackets, with the letters indicating the method of drawing, is the number of the scale to which the section of the figure is drawn.

III. Taxonomy of the Nymphs.

1. Introduction.

Classification of both adult and nymphal stoneflies is based on the external anatomy, which has been studied by many workers, most of whom have described only the adults. Hoke (1924) and Wu (1923) have, however, also dealt with the nymphs, Hoke with the head and mouth-parts of several species, and Wu with the nymphs of *Nemoura*. The nymphs differ little from the adults, the chief differences being the absence of wings and genitalia, and the fact that, in the Perlodidae and Perlidae, the mouth-parts are not reduced.

Klapálek (1909) and Enderlein (1909) have both separated the stoneflies into two sub-orders using mouth-parts as their criteria. Klapálek based his division of the group on the shape of the maxillary palps, which are either subuliform (Setipalpia) or filiform (Filipalpia), and Enderlein used the development of the mandibles in the adult, which are reduced in the Holognatha and fully developed in the Systellognatha. Neither of these arrangements seems to be satisfactory in all parts of the world, but both work well in Europe, and, in this continent, the point of division of the order is the same, so that the names proposed by each author are synonymous. It is not proposed to adopt either of these arrangements of the order, but it is convenient to refer to them here, as there are marked differences between the nymphs of the two sub-orders. In Europe in the Setipalpia Klapálek (Subulipalpia of some authors) are the families Perlodidae and Perlidae, both of which belong to Enderlein's Systellognatha, and in the Filipalpia Klapálek (= in Europe the Holognatha of Enderlein) are the families Taeniopterygidae, Capniidae, Leuctridae, and Nemouridae.

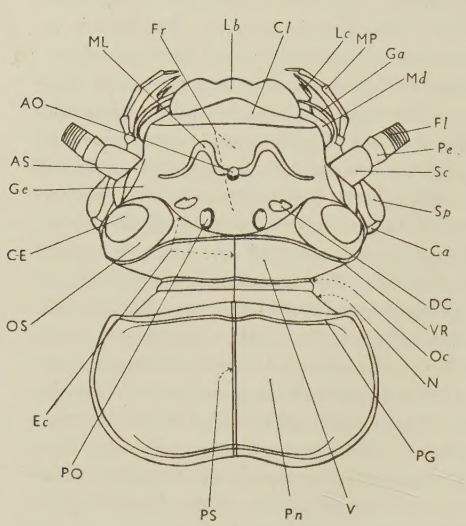
2. The Plecopteran nymph.

The head (fig. 1A) is prognathous, and well developed, being more or less flattened dorso-ventrally. The epicranial suture (Ec) is distinct, and extends almost to the base of the antenna on each side. The occiput (Oc) is separated from the vertex (V), and the clypeus (Cl) is a narrow, often membranous, sclerite separated from the frons (Fr) by a suture. The genae (Ge) are not separated from the frons, so that almost the whole of the top of the head is one sclerite. In all forms there is a well-developed antennary sclerite (AS), and in some, e.g., *Perla*, there is an ocular sclerite (OS) surrounding the compound eye (CE). The compound eyes, which are large and present at eclosion, occupy a large part of the lateral margin of the head. On the frons are three ocelli (AO and PO), and also a small callosity (DC) on each side between the lateral ocellus and the base of the antenna. These callosities overlie the point at which the dorsal arm of the tentorium touches the head capsule, and vary considerably in shape throughout the order; they are often differently coloured from the rest of the head capsule, and so form part of the head pattern. I am indebted to Dr. A. D. Imms, F.R.S., for suggesting the term dorsal callosities for these structures to replace the terms of Hoke (1924) and Kühtreiber (1934), who both mention them, but do not use them as taxonomic characters. In front of the anterior ocellus in many forms is an M-shaped line (ML), the M-line of many authors, which, although not important structurally, is of use in classification. It is often differently coloured from the rest of the frons, and, in those species with clothing hairs, is glabrous. Ventrally most of the head is covered by the mouth-parts; at the base of the mandibles there is a small mandibular sclerite.

The appendages of the head are of the type found in the Orthoptera. The antennae are setaceous and have 50–100 or more joints in the full-grown nymphs, the number varying with the species. The basal joint or scape (Sc) is large and usually covered with bristles. The second joint or pedicel (Pe) is about half the diameter of the scape, and narrower at the base than at the tip, which usually bears a crown of bristles. Both these joints are about as long as wide. There follow a large number of joints, the basal ones being much wider than long, but they become increasingly long towards the tip of the flagellum (Fl), where they are 3 or 4 times as long as wide in many species. All these joints bear distal crowns of bristles. In many forms the basal joints of the flagellum are fused, so that it appears as though the short segments were preceded by a longer one. In *Leuctra geniculata* several joints of the flagellum bear long bristles and chitinous processes (fig. 13K), and in *Brachyptera* and *Rhabdiopteryx* (Kühtreiber, 1934) each joint of the flagellum bears a pit distally, in which lie chitinous sensillae (fig. 2A). Similar knob-like sensillae are present among the bristles on the antennal joints of other species (fig. 2B), and Kühtreiber (1934) has suggested that their form and arrangement be used taxonomically. Unfortunately, to see them involves making a balsam mount, and where species are not easily separable by other means no concrete differences can be found in the antennae. The labrum is simple, being very transverse in the Setipalpia, and subquadrate in the Filipalpia. It has a close fringe of small hairs distally, and scattered bristles dorsally; on the ventral side it is often closely covered with fine hairs. The mandibles are well developed, and of two types. In the Setipalpia they are symmetrical and elongate, bearing several sharp teeth; on the inner margin there is a thick fringe of bristles, and on the dorsal surface two or three parallel lines of small bristles; there is no sign of a prostheca. In the Filipalpia the mandibles are short and stout, and slightly asymmetrical, so that they meet in an oblique line; the prostheca is well developed, and bears a series of curved spines or ridges, proximal to which is a small brush of hairs. In both types of mandible the ginglymus and condyle are well developed. The maxillae bear five-jointed palps, which taper to a point in the Setipalpia and are filiform in the Filipalpia. In *Chloroperla* the fifth joint is reduced (fig. 8F). The basal joints of these palps usually bear bristles, and the tip of the fifth joint has a very thin

patch of cuticle, on which occur small boss-like sensillae. The cardo is divided in two, and the palpifer is fused to the stipes; in many forms a sub-galea is present. The lacinia is stout and pointed, bearing two or more teeth at the tip, in *Perla* the second tooth is articulated; in all forms except *Perlodes* there is a fringe of bristles down the inner side; this sclerite is divided into distal and proximal parts. The galea is elongate and two-jointed, the distal joint being the longer. The shape is usually that of a finger and there are a few bristles at the tip, but in *Chloroperla* it is filiform and bears one long distal bristle, and in *Brachyptera* it narrows rapidly towards the tip, which bears a complex comb of bristles (fig. 2D). The hypopharynx is well developed in all forms, and lies closely adpressed to the labium; it is usually a simple sac-shaped structure covered with fine hairs, but may be bi- or trilobed in *Rhabdiopteryx* (Kühtreiber, 1934). The labium of the Filipalpia resembles that of the cockroach except that the palpigers are fused to the prementum, and the mentum is reduced to a narrow strip in all except *Capnia* (fig. 11H). The glossae and paraglossae bear fine hairs at the tip, and at the tip of the palp is a structure like that on the maxillary palp. In the Setipalpia the glossae are reduced and the paraglossae are large and sickle-shaped. The shape of the submentum varies considerably with the species, and in *Perla cephalotes* the anterior corners are separated off by sutures (fig. 6G). Lestage (Rousseau, 1921) has used the presence of a small evagination at the tip of the paraglossae as a generic character for distinguishing *Isogenus*, but this structure, which is similar to that at the tip of the palps, is present also in *Perlodes*, *Dictyopterygella* and *Isoperla*.

The thorax of some adult stoneflies, as Crampton (1914) has pointed out, is primitive. The nymphal thorax (fig. 1 A to E) resembles that of the adult, but is simplified. In the neck region there are two pairs of sclerites, one dorsal pair (DN), and one ventral pair (VN). The dorsal pair is not present in all genera, but is easily seen in *Isoperla*, *Capnia*, and *Leuctra*. The pronotum (Pn) is a single plate of varying shape, bearing a median suture, and, in the Setipalpia, bearing a marked groove (PG) just inside the margin. Many forms have a fringe of bristles round the sides and part of the front and hind margins of the sclerite. In the Filipalpia the groove is absent or poorly developed, as in the Nemouridae. The pleural region of the prothorax is poorly developed (fig. 1C); a small lateral plate (Ep) probably represents the fused episternum and epimeron, below which lies the trochantin (Tn); there is a small meron (Me) attached to the coxa (C). The meso- and metathorax resemble one another. In all forms except *Capnia* (fig. 1B), where there is a suture between the developing wing pads (WP) and the notum, the nota and wing pads are fused into one plate, which has a median longitudinal suture (MS). The postnotum (Pt) seems to be absent in many forms, but in *Capnia*, *Leuctra*, and *Protonemura* it is represented by a small sclerite on each side behind the notum. The pleural region of these segments (fig. 1C) resembles that of the prothorax, but the episternum (Es) and the epimeron (Em) are separated by a suture. The sternal region of the thorax is difficult to make out in all forms except *Perla* and *Leuctra* owing to the light chitinisation, but it seems that, except in *Leuctra*, the sternites are all fused into one ventral plate (fig. 1E, St), on either side of which, just below the episternum, lies a latero-sternite (Ls). In forms other than *Perla* it is impossible to be quite sure that the sternum is not continuous with these plates across an area of extremely thin cuticle, but in *Perla*, where the cuticle is hard, they are separate sclerites. In the adult, where the sternal region is well developed, these plates fuse with the eusternum, which becomes separated from the other sclerites. In *Leuctra* (fig. 1D) it is possible to see much of the sternal structure owing to somewhat heavier chitinisation. In the prothorax the sternum is divided into three plates, the presternum (Pr), eusternum (Eu) and sternellum (Sl), the last of which bears conspicuous apodemes (SA). Behind the sternellum in the mesothorax is a small sclerite the poststernellum (Pl), on either side of which lies a sclerite (In), which is probably intersegmental. In the prothorax the poststernellum is absent, only the intersegmental sclerites being present. In the metathorax the eusternum and sternellum are fused, and the poststernellum and intersegmental sclerites are absent.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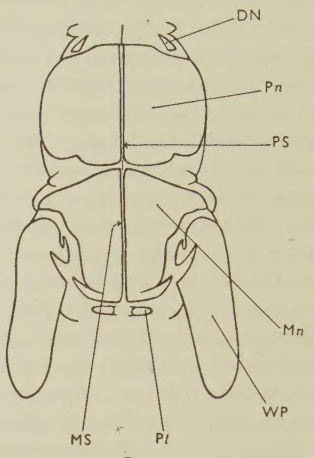
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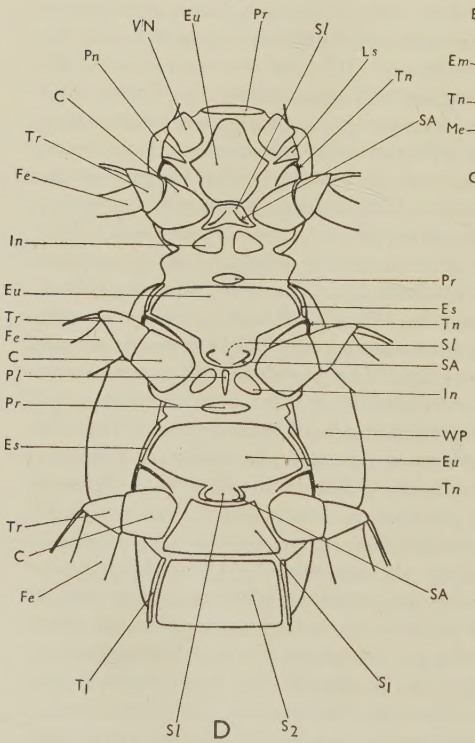
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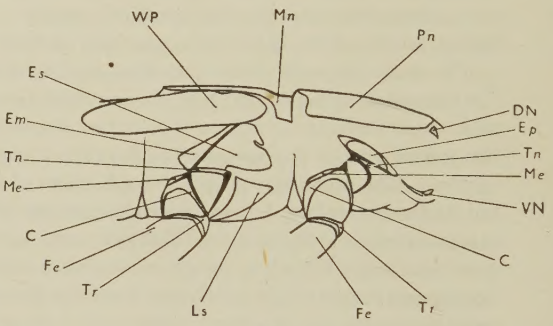
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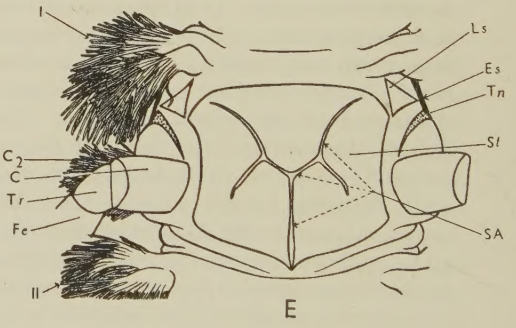
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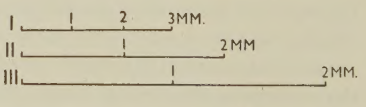

I
1
2
3MM.
II
2MM
III
2MM.

I

Latero-sternites (Ls) are only developed in the prothorax, where they are fused to the episternum; in the meso- and metathorax the eusternum is a continuous plate extending to the episternum on each side.

The wing pads (fig. 1 B to D, WP) are simple sac-shaped evaginations of the cuticle, and vary in shape and the angle at which they are set to the body according to the genus. They appear early in the life of the nymph, and when only about half-grown the wing tracheation can be clearly made out, being more easily seen on the ventral side in the heavily armoured Perlodidae and Perlidae. Shortly before emergence they become quite black owing to the crumpled wings inside them. In species having short-winged males the wing pads are very much smaller than those of the female, and in male *Capnia nigra* nymphs they do not reach to the posterior margin of the notum (fig. 11A).

The legs are well developed and stout, the coxa and trochanter being short, and the tibia slightly longer than the femur. The femur is wide and flattened in *Perlodes* and *Perla*, and in all forms it is wholly or partly grooved ventrally to receive the cylindrical tibia. There are two terminal spines ventrally on the tibia. In many forms, notably *Perlodes* and *Perla*, the femur and tibia bear a dense fringe of hairs posteriorly. The tarsus is three-jointed, the proportional lengths of the joints being of great taxonomic importance. Two stout claws, which may be toothed at the base, are borne at the tip of the tarsus. Down the middle of the anterior face of the femur and tibia runs a line, similar to the M-line on the frons in that it never bears any hairs or bristles and may be differently coloured from the surrounding cuticle.

The *abdomen* is simple and cylindrical in most forms, but flattened in *Perla*; it has ten joints and traces of an eleventh, and bears long setaceous cerci. The first segment is always divided into tergum and sternum, the sternum being closely associated with the sternites of the metathorax (fig. 1D). The second segment also has a separate tergum and sternum, but the terga and sterna of segments posterior to this may or may not be fused into a complete ring. The number of segments which are so fused has been found to form a good and easily seen taxonomic character. In *Brachyptera* the sterna of all but the last few segments are soft and membranous. The tenth segment is always fused into a complete ring, but in the Filipalpia the sternum is very narrow and lightly chitinised, and appears at first sight to be absent. Behind it lie the paired sub-anal plates, which may represent the eleventh sternum; in *Perla* these structures bear filamentous gills, and in other forms their shape is taxonomically important. The posterior margin of the tenth tergum is often drawn out posteriorly into a lobe. In many genera the eighth and ninth sterna, and

Fig. 1.—General structure. A, Head and pronotum of *Perla carlukiana* in dorsal view (I, s); B, Pro- and mesothorax of *Capnia nigra* in dorsal view (III, s); C, Pro- and mesothorax of *Capnia nigra* in lateral view (III, s); D, Thorax of *Leuctra geniculata* in ventral view (II, s); E, Mesothorax of *Perla carlukiana* in ventral view, the left gill-bunches and the posterior part of right gill-bunch II being omitted (I, s).

AO = anterior ocellus, AS = antennary sclerite, C = coxa, Ca = cardo, CE = compound eye, Cl = clypeus, C2 = pleural gill-bunch C2, DC = dorsal callosity, DN = dorsal cervical sclerite, Ec = epicranial suture, Em = epimeron, Ep = fused episternum and epimeron, Es = episternum, Eu = eusternum, Fe = femur, Fr = frons, Fl = flagellum, Ga = galea, Ge = gena, In = intersegmental sternite, Lb = labrum, Lc = lacinia, Ls = latero-sternite, Md = mandible, Me = meron, ML = M-line, Mn = mesonotum, MP = maxillary palp, MS = mesonotal suture, N = neck, Oc = occiput, OS = occipital suture, Pe = pedicel, PG = pronotal groove, Pl = post-sternellum, Pn = pronotum, PO = posterior ocellus, Pr = presternum, PS = pronotal suture, Pt = postnotum, SA = sternal apodemes, Sc = scape, Sl = sternellum, Sp = stipes, St = fused sternites, S_1 = 1st abdominal sternum, S_2 = 2nd abdominal sternum, Tn = trochantin, Tr = trochanter, T_1 = 1st abdominal tergum, V = vertex, VN = ventral cervical sclerite, VR = vertex ridge (characteristic of *Perla*), WP = wing pad, I = pleural gill-bunch I, II = pleural gill-bunch II.

often also the sub-anal plates, become modified in the older nymphs owing to the developing genitalia, thus enabling the sex of the nymph to be determined.

The cerci, which are inserted just above and slightly to the side of the sub-anal plates, are long and setaceous, having from about twenty joints in *Chloroperla* nymphs to as many as sixty in *Brachyptera*. The number of joints increases with age in all species, being only three in the first instar of *Perla*, *Chloroperla*, *Taeniopteryx*, *Protonemura*, and *Nemoura* and four in *Leuctra*. Round the apex, or slightly proximal to the apex, of each segment is a whorl of bristles, and in many forms there are scattered hairs on the segments. In the Perlodidae, *Isoperla* and *Taeniopteryx*, there is a dense fringe of long hairs running along the dorsal side of the cercus (fig. 2I).

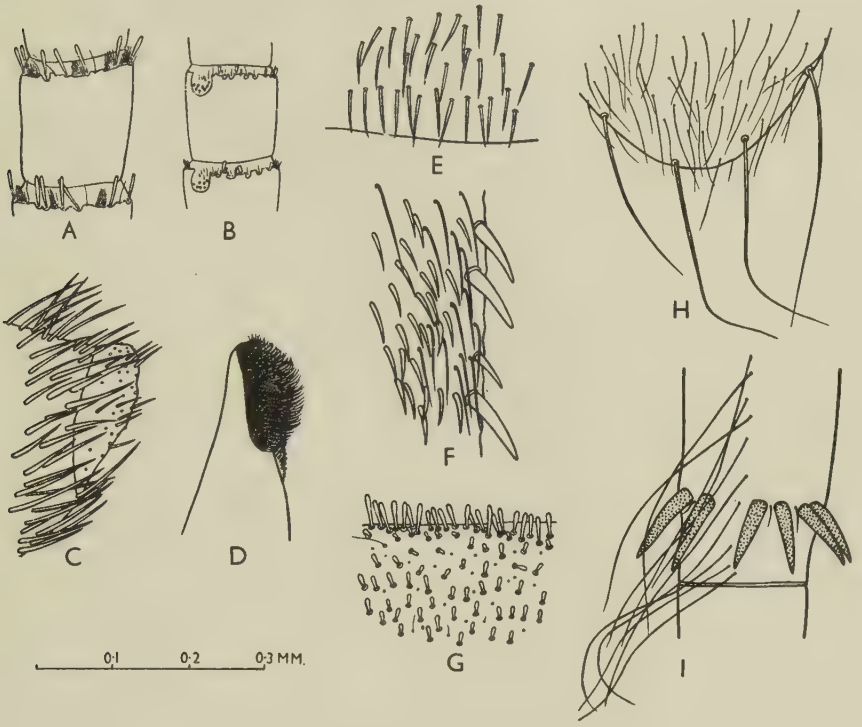
Hairs and bristles are found on some part of the body of all plecopteran nymphs, and are of numerous types which grade into one another. In the following keys and descriptions the terms hair, bristle, and clothing hair have been used. Although difficult to define precisely, these structures are more or less distinct, if examined under a low-power magnification. *Hair* refers to long thin setae such as those that form the fringe to the legs and cerci of *Perlodes*, *Dictyopterygella*, and *Perla* (fig. 2I). *Bristle* refers to stout tapering setae such as occur on the legs and nota of some species (fig. 2 C and F), and these are arbitrarily termed fine or stout bristles. In addition, the term bristle has been used for the Indian-club-shaped setae in the Nemouridae (fig. 2G), and the bristle-like sensillae found throughout the order. No name has been given to the disc-shaped sensillae found on the intersegmental membrane of the Perlodidae, Perlidae, and *Brachyptera*, and in the abdomen of *Capnia*. The term *clothing hair* may include either of the above types, and refers to hairs or small bristles which form a uniform covering to the whole or part of a sclerite (fig. 2 E and H); such a formation is typical of the Perlidae, where some or all of the bristles involved may be black, and so show clearly against pale areas of the background (fig. 2F).

Tracheal gills, which are tubular or filiform evaginations of the body wall containing tracheae, occur on some part of the body of the nymphs of many genera. The position of such gills and their general structure are important generic characters. Gills may be present on almost any part of the body, and even occur on the submentum in some American species of *Perlodes* (Claassen, 1931). In Europe four types only are found: *Pleural gills* occur in *Perla*, where there are two bunches of filamentous gills on the side of each thoracic segment, one bunch in the intersegmental membrane behind the segment, and one just above the coxa. The former bunch is referred to here as the intersegmental gill, each being referred to as gill-bunch I, II, or III, according to the thoracic segment to which it belongs (fig. 1E, I and II), and the latter bunch, which is here called the supra-coxal gill-bunch, is similarly referred to as gill-bunch C1, C2, or C3 (fig. 1E, C2). *Anal gills* are also typical of *Perla*, being bunches of filamentous gills arising from the tips of the reduced sub-anal plates (figs. 5 B and C and 6 B and C). *Coxal gills* occur only in the genus *Taeniopteryx*, and are single stout filamentous structures arising from the inner side of each of the coxae (fig. 9B). Each gill appears to be three-jointed, each joint being retractable. *Prosternal gills* occur in *Amphinemura* and *Protonemura*. They are sausage-shaped structures (fig. 14D) or stalked bunches of a few filaments (fig. 15D) which arise on each side of each ventral neck sclerite.

In those forms which have bunches of gills, the number of filaments increases as the nymph grows, and although gills appear early in the life of the nymph, in some forms, such as *Taeniopteryx* and *Protonemura*, they are absent from the first instar.

The coloration and pattern of nymphs have often been used as a means of separating species, and have formed the greater part of most of the published descriptions; but they are not altogether reliable as means of identification, because there is considerable variation, and because the young stages may be differently coloured and marked from the well-grown nymphs. Also, shortly before the nymph is about to emerge, a dark-coloured

pattern may appear, due to underlying adult structures. Neeracher (1910) describes and figures a nymph of *Leuctra klapaleki* Kemp. (= *fusciventris* Steph.) in this condition, and gives the impression that such coloration is typical of the nymph. In this genus, as in *Capnia*, the markings are deceptively unlike those of the adult, but if the emergence of the adult is watched, it will be seen that the newly emerged adult is white with a complex



2

Fig. 2.—Microscopic structure. A, Portion of the antenna of *Dictyopterygella bicaudata*, showing the arrangement of sensillae (cl); B, Portion of the antenna of *Brachyptera risi*, showing the pit containing sensillae at the tip of each joint (cl); C, Tip of the paraglossa of *Dictyopterygella bicaudata*, showing bristles and the evagination on which are small sensillae (cl); D, Tip of the galea of *Brachyptera risi*, showing the comb of bristles (cl); E, Part of the posterior margin of an abdominal tergum of *Leuctra hippopus*, showing clothing hairs of the bristle type (cl); F, Part of the margin of the mesonotum of *Perla carlukiana*, showing pale-coloured and black clothing hairs of the bristle type (cl); G, Part of the front margin of the prothorax of *Protonemura meyeri*, showing the round ended bristles (cl); H, Tip of a wing pad of *Chloroperla torrentium*, showing fine bristles and clothing hairs of the hair type (cl); I, Part of a joint of the cercus of *Dictyopterygella bicaudata*, showing the whorl of stout bristles near the tip of the segment and the dorsal fringe of long hairs (cl).

black pattern, and slowly darkens until the pattern is obscured. In view of these considerations, coloration has been used in the following keys only as a secondary character, and the range of variation found has been indicated in the descriptions.

3. Remarks on the keys and descriptions, with a key to the genera.

Identification of the species of many stonefly nymphs is a matter of some difficulty, partly because of the extreme similarity of the young stages, and

partly because the species are so variable. Kühtreiber (1934) in discussing this variability suggests that species should always be separated on positive and negative, and not on comparative, characters, but this is often impossible because such characters cannot be found. As far as possible all characters given in the keys and descriptions have been examined on several hundred specimens from various localities, and where possible from various parts of Britain. Specimens have been found that do not entirely agree with the descriptions given, but these are few in proportion to those that do, and were always accompanied by normal specimens. Accordingly, it cannot be emphasised too strongly that, in making a specific identification, particularly of small specimens of the genus *Chloroperla* and the families Leuctridae and Nemouridae, several specimens from the same locality should be examined.

In the young nymphs those characters which are best used to separate the older nymphs are frequently difficult to see, and there are often other more obvious characters which disappear as the nymphs grow. For this reason two keys (three in the genus *Nemoura*) have been made to each set of genera or species, for use with specimens above and below a certain size; specimens of this size, chosen arbitrarily for convenience in the construction of keys, can be identified by using either key. The size referred to is the length of the nymph from the front of the labrum to the base of the cerci. There is also a minimum size given; below this it is not possible to use the keys, or even in some genera to make any specific determination unless one is thoroughly familiar with the species in all other stages.

Lestage (Rousseau, 1921) has given a key with which the nymphs may be placed in families, but unfortunately such a key is difficult to make use of because of the difficulty of separating the Perlodidae and Perlidae, and it has been thought better to adopt the practice of Klapálek (1909) and Kühtreiber (1934) and give a key only to the genera. The genera are then described separately under family headings, and keys to the species are given where possible. Those genera and species which are on the British list (Lucas, 1932) but whose existence in Britain is doubtful (Hynes, 1940) are not included in the keys, even if descriptions of the nymphs are available in the literature, because, as explained later, there is some doubt as to the reliability of the characters proposed in these descriptions. The keys given here are intended to apply only to specimens taken in Britain, because they have been worked out only on British material, and use has been made of previously undescribed characters which may not apply to species outside the British Isles. Such characters have been used because they are easier to see, and appear to be more fundamental than some of the characters used by previous workers, whose keys have often proved difficult to use. Nymphs of some species recorded from Britain have not been obtained; these are included where possible in the descriptions, but not in the keys. This involves omitting *Isogenus* (three records) and *Rhabdiopteryx* (one record) from the generic key, but, as there is considerable doubt as to the validity of the generic characters proposed for them (Rousseau, 1921, and Kühtreiber, 1934), this is considered advisable.

Numerous isolated descriptions of nymphs have been published, some of them appearing to be extremely thorough (*e.g.*, Klapálek, 1904, Koponen, 1917, and Kühtreiber, 1931), but only when definite attempts were made to separate species have reliable characters been given. Such descriptions are therefore useless unless they are comparative, specific differences usually being such that they are not mentioned in a general description. The references given under each specific name refer to descriptions of the nymph.

Throughout this paper the subgenera of *Nemoura* have been treated as genera, as is the practice of some European workers (Kimmins, 1940), although, as was explained in an earlier paper (Hynes, 1940), this procedure is not entirely justified, because the American species of the genus will not fit into this arrangement (Needham and Claassen, 1925). It is done here for convenience in identification, and because the nymphs of these subgenera are quite distinct one from another.

A collection of nymphs, together with adults collected or bred from the same locality, has been deposited at the British Museum, and a similar collection has been deposited at the Wray Castle Laboratory of the Freshwater Biological Association of the British Empire. The specimens in the British Museum may be regarded as nymphal syntypes. The rule applying to adult insects, that one specimen should be fixed as a type, has not been followed, because many species show such great variability, and because it is not the usual procedure in describing the young stages of insects. Accordingly, unless otherwise stated, the descriptions given here have been made from a long series of nymphs usually numbering from fifty to several hundreds, where possible from several localities, and only some of these nymphs have been set aside as types. In recording localities the vice-county system proposed by Balfour-Browne (1931, *Ent. mon. Mag.* **67** : 183–193) has been used.

All the characters mentioned in the keys and descriptions can be seen, in specimens preserved in 2% formaldehyde, with a magnification of less than × 50. In the genus *Leuctra*, however, it may be found desirable to mount small specimens in balsam in order to see the arrangement of the bristles; it adds to the ease of identification if they are first stained for a few minutes in carbol-fuchsin.

Keys to the genera.

Specimens over 5 mm.

1(10). Glossae reduced (figs. 3–8G). Labrum more than twice as wide as long (figs. 3–8D). 10th abdominal sternum well developed (figs. 3–8 B and C).

2 (3). Bunches of pleural gills present on the thorax (figs. 5A and 6A) *Perla* Geoff. (p. 480).

3 (2). No gills present.

4 (5). Last joint of the maxillary palp reduced, only about ¼ as wide as the preceding joint (fig. 8F) . . . . . *Chloroperla* Newm. (p. 488).

5 (4). Last joint of the maxillary palp normal, more than ¼ as wide as the preceding joint (figs. 3F, 4F, and 7F).

6 (7). Abdominal segments 1–4 divided into tergum and sternum (fig. 3I). Lacinia narrowing evenly towards the tip, only one or two fine bristles on the inner margin (fig. 3F) . . . . . *Perlodes* Banks (p. 474).

7 (6). Abdominal segments 1 and 2 only divided into tergum and sternum, segments 3–4 fused into a complete ring (fig. 4I). Lacinia emarginate on the inside just below the tip, with a fringe of bristles on the inner margin (figs. 4F and 7F).

8 (9). Sub-anal plates blunt, with a few curved bristles in older specimens (figs. 4 B and C). Body covered with scattered bristles. *Dictyopterygella* Klap. (p. 477).

9 (8). Sub-anal plates long and pointed, covered with black clothing hairs (fig. 7C). Body thickly covered with black clothing hairs *Isoperla* Banks (p. 485).

10 (1). Glossae well developed, as long as paraglossae (figs. 9–12H, 14I, 15I, 16H, and 18H). Labrum less than twice as wide as long (figs. 9–12D, 14E, 15E, 16D, and 18D). 10th abdominal sternum reduced to a narrow lightly chitinised strip (figs. 9C, 10 and 11 B and C, 12J, and 14, 15, 16, and 18 B and C).

11(14). Each joint of the tarsus longer than the preceding joint (figs. 9I and 10I).

12(13). A 3-segmented retractile filamentous gill present on the inner side of each coxa (fig. 9B). Abdominal terga with spiniform projections on the hind margin (fig. 9J) . . . . . *Taeniopteryx* Pict. (p. 492).

13(12). Coxae without gills. Abdominal terga normal, without projections *Brachyptera* Newp. (p. 494).

14(11). Joint 2 of the tarsus shorter than joint 1 (figs. 11I, 12I, 14J, and K, 16K, and 18J).

15(18). Cylindrical elongate nymphs, wing pads sub-parallel to the body (figs. 11A, and 12 A–C). Hind leg when stretched back alongside the abdomen not quite reaching its tip.

16(17). Abdominal segments 1–9 divided into tergum and sternum (fig. 11C). Sub-anal plates wider than long (figs. 11 B and C). *Capnia* Pict. (p. 498).

17(16). Abdominal segments 1–4 only divided into tergum and sternum, segments 5–9 fused into a complete ring (fig. 12J). Sub-anal plates longer than wide (fig. 12J) . . . . . *Leuctra* Klap. (p. 500).

18(15). Stout nymphs, wing pads set obliquely to the body (figs. 14–16A, and 18A). Hind leg when stretched back alongside the abdomen greatly overreaching its tip.

19(22). Prosternal gills present.

20(21). Prosternal gills composed of three sausage-shaped structures on each side (fig. 14D) . . . . . *Protonemura* Kemp. (p. 507).

21(20). Prosternal gills composed of two bunches of 5–8 filaments on each side (fig. 15D) . . . . . *Amphinemura* Ris (p. 510).

22(19). No prosternal gills present.

23(24). Joint 1 of the hind tarsus about $\frac{1}{4}$ as long as joint 3 (fig. 16K). No distinct transverse row of bristles on any of the femora; if bristles are present they are scattered (figs. 16 A and I). *Nemoura* Latr. s.str. (p. 513).

24(23). Joints 1 and 3 of the hind tarsus sub-equal (fig. 18J). Femora of at least some legs with a transverse row of long bristles dorsally shortly before the tip (fig. 18I) . . . . . *Nemurella* Kemp. (p. 518).

Specimens 1–5 mm.

1(10). Glossae reduced (figs. 3–8G). Labrum more than twice as wide as long (figs. 3–8D). 10th abdominal sternum well developed (figs. 3–8 B and C).

2 (3). Bunches of filamentous gills on the sides of the thorax or on the sub-anal plates, or on both (in very small specimens each bunch may be represented by only one or two filaments). Head with a distinct transverse ridge behind the eyes . . . . . *Perla* Geoff. (p. 480).

3 (2). No gills present. Head without a transverse ridge.

4 (5). Last joint of the maxillary palp reduced, $\frac{1}{4}$ to $\frac{1}{3}$ as wide as the preceding joint (fig. 8F). . . . . *Chloroperla* Newm. (p. 488).

5 (4). Last joint of the maxillary palp normal, more than $\frac{1}{3}$ as wide as the preceding joint (figs. 3F, 4F, and 5F).

6 (7). Head in front of a line between the antennae and meso- and metanota distinctly darker coloured than the rest of the body, abdomen pale. Abdominal segments 1–4 divided into tergum and sternum (fig. 31). *Perlodes* Banks (p. 474).

7 (6). Colour uniform pale grey, or, if the front part of the head and the meso- and metanota are darker coloured than the rest of the body, abdominal terga 1–6 are darkened also. Abdominal segments 1 and 2 only divided into tergum and sternum, segments 3–4 fused into a complete ring (fig. 4I).

8 (9). Head in front of the epicranial suture, meso- and metanota, and abdominal terga 1–5 dark grey, rest of the body pale yellow. Nota with a few bristles . . . . . *Dictyopterygella* Klap. (p. 477).

9 (8). Colour uniform pale grey. Nota covered with distinct black clothing hairs and bristles, which look disproportionately large in small specimens . . . . . *Isoperla* Banks (p. 485).

10 (1). Glossae well developed, as long as paraglossae (figs. 9–12H, 14I, 15I, 16H, and 18H). Labrum less than twice as wide as long (figs. 9–12D, 14E, 15E, 16D, and 18D). 10th abdominal sternum reduced to a narrow lightly chitinised strip (figs. 9C, 10 and 11 B and C, 12J, and 14, 15, 16, and 18 B and C).

11(14). Each joint of the tarsus longer than the preceding joint (figs. 9I and 10I).

12(13). A 3-segmented retractile filamentous gill present on the inner side of each coxae (fig. 9B). . . . . *Taeniopteryx* Pict. (p. 492).

13(12). Coxae without gills . . . . . *Brachyptera* Newp. (p. 494).

14(11). Joint 2 of the tarsus shorter than joint 1 (figs. 11I, 12I, 14J, and K, 16K and 18J).

15(18). Cylindrical elongate nymphs. Hind leg when stretched back alongside the abdomen not quite or just reaching its tip.

16(17). Abdominal segments 1–9 divided into tergum and sternum (fig. 11C). Sub-anal plates wider than long (figs. 11 B and C). *Capnia* Pict. (p. 498).

17(16). Abdominal segments 1–4 only divided into tergum and sternum, segments 5–9 fused into a complete ring (fig. 12J). Sub-anal plates longer than wide (fig. 12J) . . . . . *Leuctra* Klap. (p. 500).

18(15). Stout nymphs. Hind leg when stretched back alongside the abdomen greatly overreaching its tip.

19(22). Prosternal gills present.

20(21). Prosternal gills composed of three sausage-shaped structures on each side (fig. 14D). . . . . *Protonemura* Kemp. (p. 507).

21(20). Prosternal gills composed of two bunches of filaments on each side (fig. 15D). (The number of filaments decreases with the size of the nymph from 5–8 to as few as 2 in the outer and 1 in the inner bunch in some specimens, but they are always filamentous and never sausage-shaped.) . . . . . *Amphinemura* Ris (p. 510).

22(19). No prosternal gills present.

23(24). No distinct transverse row of bristles on any of the femora; if bristles are present they are scattered (figs. 16 A and I).
Nemoura Latr. s.str. (p. 513).

24(23). Femora of at least some legs with a transverse row of long bristles dorsally shortly before the tip (fig. 18I) *Nemurella* Kemp. (p. 518).

4. Perlodidae Klapálek, 1909.

The nymph of one species belonging to this family, *Perlodes microcephala* Pict., has been known for over a century (Pictet, 1833), and several species have been described since. Separation of this family from the Perlidae is a matter of some difficulty, although the individual genera of each can be readily recognised. Lestage (Rousseau, 1921), who divided the Perlidae Klap. into Perlidae and Chloroperlidae, separated his Perlidae, containing only the genus *Perla*,

on the presence of gills, and then separated the PERLODIDAE from CHLOROPERLIDAE on the maxillary palp. He stated, following Klapálek (1909), that in the PERLODIDAE the third joint of the palp is never shorter than the fourth, the fifth being non-acuminate, while in the CHLOROPERLIDAE the fourth joint is longer than the third and the fifth is acuminate. This character is highly unsatisfactory because of the very small differences of proportion, and because in young specimens of the PERLODIDAE the fifth joint of the palp is definitely acuminate. A character more easily seen is the lack of clothing hairs in the PERLODIDAE, only scattered bristles being present, while in the PERLIDAE clothing hairs cover most of the body.

The family is therefore characterised by the large size, the reduced glossae (figs. 3G and 4G), the wide labrum which is more than twice as wide as long (figs. 3D and 4D), the well-developed 10th abdominal sternum (figs. 3 B and C and 4 B and C), and the absence of gills and clothing hairs. In all forms tarsal joints 1 and 2 are short, and joint 3 is long (figs. 3H and 4H), there is a dense fringe of long hairs down the posterior margin of the femur, tibia, and tarsus of each of the legs (figs. 3A and 4A), and the femur is somewhat dorso-ventrally flattened.

Three genera are listed as British (Lucas, 1932), but *Isogenus nubecula* is rare.

Perlodes Banks, 1903.

Dictyopteryx Klapálek, 1906.

Pictet (1833) first described a nymph of this genus briefly, and later (1842) amplified this description, but he confined himself almost entirely to colour. Klapálek included the genus in a key, but did not separate it from *Isogenus*; more recently Lestage (Rousseau, 1921), Uéno (1929), and Kühtreiber (1934) have included it in keys. Lestage based his separation on the relative widths of the head and pronotum, a character well known to vary with age (Kühtreiber, 1934), and on the proportionate lengths of the hypopharynx and paraglossae, a character which is also apt to be misleading owing to slight changes in position of these structures. Uéno also used the relative widths of the head and pronotum, and by so doing seems to have made a misidentification, in that his *Perlodes dispar* Ramb. shows a fringe of bristles on the lacinia, a character which, as Kühtreiber (1934) has shown, is not found in *Perlodes*, and has bristles on the abdominal terga, a character shown by *Dictyopterygella* (Mertens, 1921 and 1923). Kühtreiber's key, which is based on the lacinia, would therefore appear to be the most satisfactory.

The genus is characterised by the simple lacinia, which tapers gradually towards the tip and is without a fringe of bristles on the inner margin (fig. 3F), the absence in most specimens of bristles covering the posterior half of each abdominal segment (figs. 3 B and C), the tooth at the base of each tarsal claw (fig. 3H), and, at least in British material, by the fact that abdominal segments 1–4 are divided into tergum and sternum (fig. 3I). The last-named character, which is by far the easiest to see, has not been used before, and may not hold in other parts of Europe. The American species *Perlodes signata* Hag. does not show it, only segments 1 and 2 being so divided; it differs in many other respects from European species of the genus, having pleural and labial gills, and a fringe of bristles on the lacinia.

There is one species of this genus on the British list (Lucas, 1932).

Perlodes mortoni (Klapálek, 1906) (fig. 3).

? *Perlodes mortoni* Klap., Schoenemund 1930.

Size of full-grown nymph, male 18–21 mm., female 25–28 mm.

General colour dark grey to black with yellow markings above, pale yellow below. The extent of the yellow markings varies considerably, and may be as great as that shown in fig. 3A, or so reduced that the nymph appears to be quite black. The paler specimens are

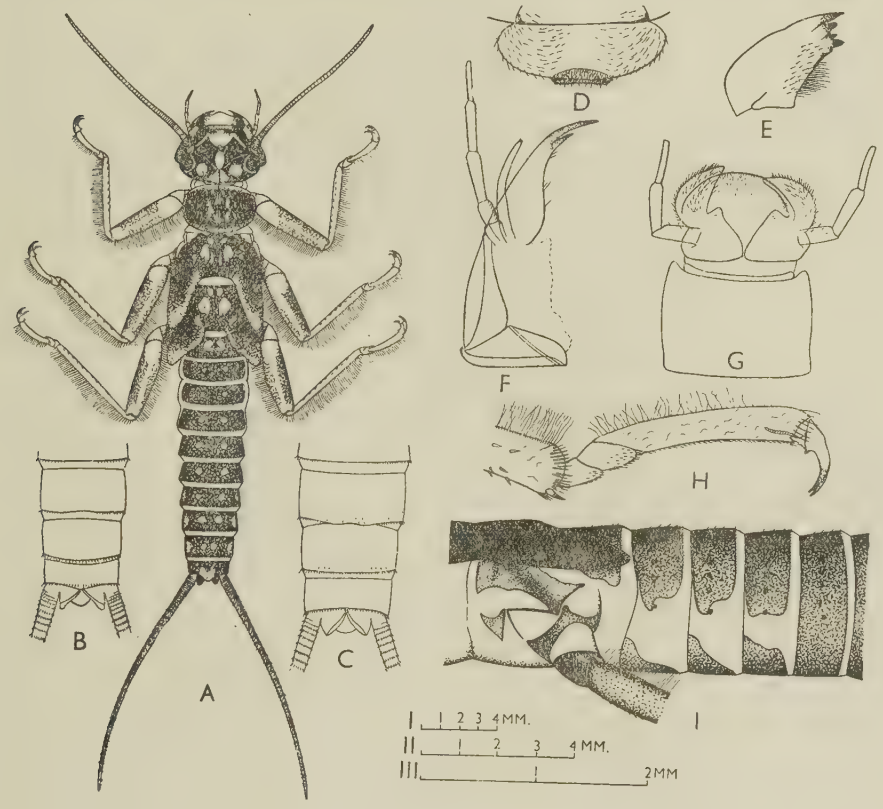


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Fig. 3.—*Perlodes mortoni*. A, Full-grown female nymph (I, m); B, Tip of full-grown male abdomen in ventral view (II, m); C, Tip of full-grown female abdomen in ventral view (II, m); D, Labrum in dorsal view (III, cl); E, Right mandible in ventral view (III, cl); F, Right maxilla in ventral view (III, cl); G, Labium with hypopharynx attached in ventral view (III, cl); H, Hind tarsus (III, cl); I, Base of abdomen in lateral view (II, m).

found on pale substrata, while the darker specimens occur on dark substrata such as are found in many small stony streams.

Head wide and flattened, wider than the pronotum. M-line, dorsal callosities, the part of the frons in front of the M-line, and the clypeus, pale yellow; the latter two areas are darkened at the sides. Between the ocelli is an oval yellow spot, and the part of the vertex round the posterior arm of the epicranial suture and a round spot on each side are often yellow also. Eyes and ocelli often bordered with yellow. Antennae light grey to yellow,

labrum yellow, darkened at the sides, cardo and stipes yellow to grey, labium yellow. Submentum subquadrate with drawn-out anterior corners.

Pronotum elliptical with a well-marked groove. In pale specimens the extreme lateral margins, a longitudinal median line, and several lateral vaguely defined outwardly concave crescents are yellow, but in dark specimens the pronotum is usually black. There is no fringe of bristles to any of the nota. Meso- and metanota with a characteristic arrangement of yellow spots, which, however, cannot be made out in dark specimens. Wing pads, which are somewhat smaller in the male than in the female, yellowish towards the tips in pale specimens.

Legs white to pale yellow. Femora slightly flattened, and with a dark smudge towards the middle, which is traversed by the yellow femoral line. Tarsi and claws strong.

Abdomen grey above and yellow below; in pale specimens there are two yellow dorso-lateral spots on each tergum, which are often larger in the posterior segments, and may fuse laterally with the pale area below. Each tergum has a fringe of small bristles on its hind margin, and very rarely there are a few scattered bristles over the hinder half of the sclerite. The fringe of bristles extends round ventrally on to the sterna in the hinder segments. In the male sternum 8 is simple, but in the female it bears a small lobe posteriorly on which are a few scattered bristles, and through which in young specimens may be seen the chitinised walls of the vagina. The sexes are distinguishable in specimens over 9 mm. Cerci rufous, nearly as long as the abdomen in full-grown nymphs, and longer in the earlier stages. Each joint has a subapical whorl of stout bristles, and a fringe of long hairs on the dorsal side.

Nymphs below 5 mm. differ greatly in colour but not in structure from older nymphs, only the bristles being fewer and much longer in proportion. At 1·5 mm. the head in front of a line between the bases of the antennae is black, as are the meso- and metanota, the rest of the body being white; ocelli are absent. As the nymph grows to about 4 mm. the white areas become pale grey and darken slowly, and at the same time the ocelli and traces of the pale marking begin to appear. At 5 mm. the marking has appeared, but is not so sharply defined as in the older nymphs, the meso- and metanota are, however, still clearly darker than the pronotum and abdomen, and this contrast does not entirely disappear until about 5·5 mm. The first instar of this species has not been obtained, but some specimens just under 1 mm. collected with slightly larger typically marked specimens of *P. mortoni*, have only three cercal joints, a character common to the first instar of many species, and are quite white.

Nymphs of this species collected in the following vice-counties have been examined: Cumberland (CU), Westmorland + N. Lancs (WL), N.W. Yorks (NY), and Durham (DM).

Nymphal syntype (light- and dark-coloured specimens), WL, Hawkshead, How Beck, 26.iv.1940, full-grown nymphs (♂, 4 ♀) (*Hynes*).

Schoenemund describes and figures the nymph of a species which he calls, with some doubt, *P. mortoni*, but which Kühtreiber (1931) believes to be *P. microcephala* (Pict.). The description, however, agrees closely with pale coloured specimens of *P. mortoni* from Britain. Kühtreiber (1934) has used head markings to separate the nymphs of *P. intricata* (Pict.) and *P. microcephala*, but unless the coloration in these species is much less variable than in British specimens of *P. mortoni*, this cannot be a reliable character. Similarly, he uses the relative lengths of cerci and abdomen, but this character can apply only to full-grown nymphs, because in all stonefly nymphs the proportionate length of the cerci varies with age. It is therefore possible only to separate *P. mortoni* from *P. microcephala*, as described by Kühtreiber, on the shape of the M-line, which is intermediate between that found in the other two species.

Dictyopterygella Klapálek, 1906.

Nymphs of this genus, which is given as a sub-genus of *Perlodes* by many workers (Schoenemund, 1927, and Klapálek, 1909), have not been included in any previously published nymphal key. Species of the genus have been described (Koponen, 1917, and Mertens, 1921 and 1923), and Mertens has suggested that the presence of scattered bristles on the latter half of each abdominal tergum is a character distinguishing the genus from *Perlodes*. Such bristles do, however, occur rarely on *Perlodes*, and are not present on young specimens of *Dictyoptergyella*.

The genus is characterised by the lacinia, which is emarginate below the tip and bears a fringe of bristles on the inner margin (fig. 4F), the presence in all specimens of scattered bristles over the posterior half of each abdominal segment (figs. 4 B and C), the tooth at the base of each tarsal claw (fig. 4H), and, at least in British material, by the fact that abdominal segments 1 and 2 only are divided into tergum and sternum (fig. 4I).

There is one species on the British list (Lucas, 1932).

Dictyopterygella bicaudata (Linnaeus, 1758) (fig. 4).

= *recta* (Kempny, 1900).

Dictyopterygella recta Kemp., Koponen 1917.
Dictyopterygella recta Kemp., Mertens 1921 and 1923.

Size of full-grown nymph, male 8·5–17·0 mm., female 19–24 mm. The size seems to be very variable, adults from different parts of Britain, and even from different parts of the Lake District, being greatly different in size; Koponen (1917) records females as small as 14 mm. It seems that specimens from the exposed rocky shores of lakes such as Wastwater (CU) are smaller than those from more sheltered localities such as Windermere (WL).

General colour grey-brown with yellow markings above, yellow below. In this species the markings show little variation.

Head wide and flattened, wider than the pronotum. Clypeus white, M-line, dorsal callosities, and an oval spot between the ocelli yellow. On the vertex a central and two lateral yellow areas, which are often darkened in the middle. Eyes and ocelli often bordered with yellow. Antennae light brown, labrum yellow or light brown with a dark spot on each side anteriorly, maxillae and labium yellow to light brown. Submentum with wide rounded lateral margins.

Pronotum elliptical with a well-marked groove. The anterior and posterior borders are black, the rest of the sclerite being marked as in pale specimens of *P. mortoni*. There is no fringe of bristles to any of the nota. Meso- and metanota with a characteristic arrangement of yellow spots, some of which are darkened in the middle. Wing pads, which are somewhat smaller in the male than in the female (fig. 4A), yellow, with a dark spot on the anal area.

Legs pale yellow. Femora slightly flattened, and with a dark smudge towards the middle, which is traversed by the yellow femoral line. Tarsi and claws strong.

Abdomen grey-brown above, yellow below, with two vague dorso-lateral yellow spots on each tergum, which are usually fused on the anterior and posterior segments; there is also a transverse row of small pale spots on each tergum. Each abdominal segment has scattered bristles over the posterior half, and a fringe of small bristles on the posterior margin of each tergum, which extends round on to the sterna in the hinder segments. In the male sternum 8 is simple, but in the female it bears a small central thickening, just anterior to which in young specimens the chitinised walls of the vagina can be seen through the sternum. The sexes are distinguishable in specimens over 9 mm. Cerci yellow, about as long as or slightly longer than the abdomen. Each joint has an apical whorl of stout bristles, and a fringe of long hairs on the dorsal side.

Nymphs below 5 mm. differ greatly in colour but not in structure from the older nymphs, only the bristles being fewer and much longer in proportion, and the scattered bristles being absent from the abdominal segments. At 2·5 mm., which are the smallest specimens that have been obtained, the head in front of the epicranial suture, the meso- and metanota, and abdominal terga 1–5, are dark grey, the rest of the body being white. At 3 mm. the ocelli appear, and at about 4 mm. the pale areas begin to darken. At 5 mm. the marking appears

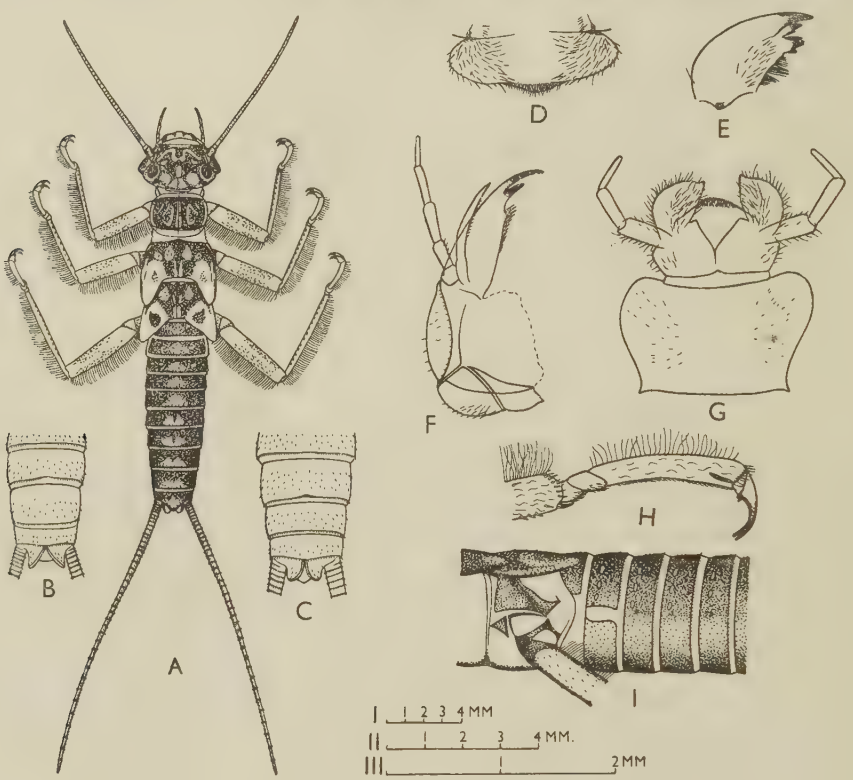

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Fig. 4.—*Dictyopterygella bicaudata.* A, Full-grown female nymph in dorsal view (I, m); B, Tip of full-grown male abdomen in ventral view (II, m); C, Tip of full-grown female abdomen in ventral view (II, m); D, Labrum in dorsal view (III, cl); E, Left mandible in dorsal view (III, cl); F, Right maxilla in ventral view (III, cl); G, Labium, with hypopharynx attached, in ventral view (III, cl); H, Hind tarsus (III, cl); I, Base of abdomen in lateral view (II, m).

and above this size the contrast between the dark and pale areas rapidly disappears, and the marking becomes more distinct; at the same time the characteristic bristles on the hinder half of the abdominal segments develop.

Nymphs of this species collected in the following vice-counties have been examined: Cumberland (CU), Westmorland + N. Lancs (WL), and Wicklow (WI).

Nymphal syntype, WL, Windermere, 26.iv.1940, full-grown nymphs (3 ♂, 3 ♀) (*Hynes*).

British specimens agree closely with descriptions by Koponen and Mertens of this species from Europe. One other species of the genus, *D. septentrionis* Klap., has been described (Koponen, 1917).

Isogenus Newman, 1833.

This genus has been placed in a generic key by Lestage (Rousseau, 1921), who based his characters on a description by Klapálek (1904) of the only European species. Unfortunately the characters proposed by him, with the possible exception of the shape of the pronotum, cannot be regarded as reliable in Britain, because *Dictyopterygella* shows a small evagination at the tip of the paraglossae and a fringe of bristles down the inner side of the galea, both of which characters Lestage describes as typical of *Isogenus*; he had no specimens of *Dictyopterygella*. Similarly Uéno (1929) placed the genus in a key, using the fact that in *Isogenus* the head is narrower than the pronotum; but, as Kühtreiber (1934) has pointed out, the ratio of width of head to width of pronotum decreases with age in *Perlodes* and other forms, and it is highly probable therefore that at some stage in its development the head of *Isogenus* is wider than the pronotum. Klapálek (1904) states that the tarsal claw is simple, but Uéno (1929) describes and figures it as toothed at the base; similarly, while Lestage says that the hypopharynx is drawn out into a blunt point, Uéno figures it as rounded. All authors agree that the lacinia is emarginate just below the tip and bears a fringe of bristles down the inner side, as occurs in *Dictyopterygella* and *Dictyogenus* (Kühtreiber, 1934), and that there is a fringe of hairs on the cercus.

From these considerations it is obvious that, in the absence of further information, the genus cannot be included in a key to the British genera. The shape of the pronotum, which is quadrate instead of elliptical as in other members of the family, could perhaps be used, but Uéno's figure shows a pronotum which is more nearly elliptical than quadrilateral, and the pronotum in Klapálek's figure, on which Lestage bases his key, is not easily distinguishable from that of *Perlodes*.

The one European species is listed as British (Lucas, 1932), because of one adult male specimen which is in the Stephens collection at the British Museum, but is without date or locality. It was suggested in an earlier paper (Hynes, 1940) that this may not be a true British species, but Mr. Kimmins has recently informed me that in the McLachlan collection, now at the British Museum, he has found a female, said to be from the Burton-on-Trent district, and a male without locality. King and Halbert (1910) state that *D. bicaudata* was often erroneously identified as *I. nubecula* in early British collections.

Isogenus nubecula (Newman, 1833).

Isogenus nubecula Newm., Klapálek 1904 and 1909.
? *Isogenus nubecula* Newm., Uéno 1929.

The following brief colour description is condensed from that of Klapálek, and may be of use in identification of the nymphs of the species, should they be found in Britain.

General colour light brown above with paler markings, pale olive green below. Head pale in front of the M-line, with a pale spot between the ocelli and pale spots on each side of the vertex. Pronotum pale all round the edge and down the median line, on each side of which is a pale *outwardly* convex crescent (cf. *Isoperla*, fig. 7A: in *Perlodes* and *Dictyop-*

terygella any crescentic pronotal marks are inwardly convex). Meso- and metanota with four round pale spots, one anteriorly, one posteriorly, and one on each side. Antennae, legs, and abdomen light brown.

5. Perlidae Klapálek, 1909.

The genera in this family are diverse in size and general structure, and as explained above (p. 473) it is not easy to find good characters on which to separate the family as a whole from the Perlodidae.

The family is characterised by the reduced glossae (figs. 5G, 6G, 7G, and 8G), the wide labrum which is more than twice as wide as long (figs. 5D, 6D, 7D, and 8D), the well-developed 10th abdominal sternum (figs. 5 B and C, 6 B and C, and 7C), and the presence of clothing hairs over most of the body. In Europe only the genus *Perla* possesses gills. In all forms tarsal joints 1 and 2 are short, and joint 3 is long (figs. 5H, 6H, 7H, and 8H), and there is a dense fringe of long hairs down the posterior margin of the femur, tibia and tarsus of each of the legs (figs. 5A, 6A, 7A, and 8A). The femur is strongly dorso-ventrally flattened in *Perla*, and less so in the other forms. In all the British species that have been obtained abdominal segments 1 and 2 only are divided into tergum and sternum, the rest being fused into a complete ring.

Three genera are listed as British (Lucas 1932).

Perla Geoffroy, 1764.

The large nymphs of this genus have been known for over a century (Pictet, 1833), and many species have since been described. Schoenemund (1912 and 1925a) has dealt fully with the grown nymphs of the German species, but has not separated the young stages.

The genus is characterised by the large size, the presence of pleural and anal gills, the normal maxillary palp (figs. 5F and 6F), and the tooth at the base of each tarsal claw (figs. 5H and 6H). Schoenemund (1925b) states that up to the eleventh week of life the nymphs of *P. cephalotes* Curt. have no gills, but Samal (1923), describing the first instar of *P. abdominalis* (Burm.), mentions gills on the metathorax. The eggs of both *P. cephalotes* and *P. carlukiana* Klap. have been hatched in the laboratory, and gills were found to be present during the first instar of both, metathoracic pleural gills being present in *P. carlukiana* and anal gills in *P. cephalotes*.

Two subgenera with three species are listed as British (Lucas, 1932), but the record of *P.* (*Perla*) *marginata* is doubtful (Hynes, 1940, and p. 485), and the species is not included in the key.

Keys to subgenera and species.

Specimens over 5 mm.

1 (2). Pronotum more than twice as wide as long (fig. 5A). Submentum with anterior corners separated off by sutures (fig. 5G). General colour red-brown to dark brown with a pattern of yellow or pale grey, last abdominal tergum uniformly dark (fig. 5A)
P. (*Dinocras*) *cephalotes* Curt. (p. 481).

2 (1). Pronotum less than twice as wide as long (fig. 6A). Submentum without anterior corners separated off by sutures (fig. 6G). General colour black with a bold yellow pattern, last abdominal tergum yellow (fig. 6A) . . . . . *P.* (*Perla*) *carlukiana* Klap. (p. 483).

Specimens 1–5 mm.

1 (2). Pronotum more than twice as wide as long. Anal gills present, being about $1\frac{1}{2}$ times as long as the 10th abdominal tergum. General colour uniform grey . . . . *P.* (*Dinocras*) *cephalotes* (Curt. (p. 481).

2 (1). Pronotum less than twice as wide as long. Anal gills absent. General colour yellow, with the edges of the nota often slightly darker *P.* (*Perla*) *carlukiana* Klap. (p. 483).

Perla (*Dinocras* Klapálek, 1907) *cephalotes* Curtis, 1827 (fig. 5).

Perla cephalotes Curt., Pictet 1833 and 1842.
Perla (*Dinocras*) *cephalotes* Curt., Klapálek 1909.
Perla (*Dinocras*) *cephalotes* Curt., Neeracher 1910.
Perla (*Dinocras*) *cephalotes* Curt., Petersen 1910.
Perla (*Dinocras*) *cephalotes* Curt., Schoenemund 1912, 1924, and 1925 a and b.
Perla (*Dinocras*) *cephalotes* Curt., Kühtreiber 1934.

Size of full-grown nymph, male 14–18 mm., female 24–31 mm. Schoenemund (1925a) records females up to 33 mm.

General colour red-brown to dark brown or almost black with yellow-grey markings above, paler below. Like *P. mortoni*, specimens from dark substrata are darker than those from paler localities. The darkening, which may render the nymph almost black, is brought about by a reduction in the extent of the pale areas and a general darkening of the ground-colour and markings.

Head very wide and flattened. M-line, two spots in front of its anterior corners on the frons, and dorsal callosities pale. Eyes and ocelli bordered with pale yellow or grey. On the vertex, behind a prominent ridge which runs transversely behind the eyes, are variable pale areas. Antennae and mouth-parts yellow-grey to brown. Submentum wide and rounded at the sides, with two semicircular pieces separated from the anterior corners by sutures.

Thorax wide and flattened, bearing pleural gills, over which project the edges of the nota. Pronotum rectangular, more than twice as wide as long, with a pale median line, and laterally a series of vaguely defined outwardly concave crescentic marks. Meso- and metanota with a characteristic arrangement of pale spots, which, like the pronotal marking, are often obscured in dark specimens. Wing pads dark coloured, smaller in the male than in the female.

Legs brown or yellow, paler below, darkened at the femoro-tibial joint and along the front margin of the femur.

Abdomen broad and flattened, uniformly brown, or, in very pale specimens, with two pale dorso-lateral spots on each tergum. In the male sternum 8 is simple, but in the female it bears an indistinct thickening on the hind margin through which in young specimens the chitinised walls of the vagina can be seen. The sexes are distinguishable in specimens over 5 mm. The sub-anal plates are reduced, and bear bunches of filamentous anal gills. The cerci are reddish, stout at the base and tapering rapidly. Each joint bears a subapical whorl of stout bristles.

The entire body is covered with clothing hairs which are mostly of the pale bristle type, but black bristles occur on the centres of the nota. The nota and abdominal terga have fringes of small stout bristles round the edges.

The gills, which are bright silver-white, occur in bunches of filaments as follows: one bunch, the anal gills, on each of the sub-anal plates; one bunch in the pleural membrane on each side behind each thoracic segment (fig. 1E) (referred to here as gill-bunches I, II, and III, according to which abdominal segment they are behind), and one bunch above each coxa (fig. 1E) (referred to here as gill-bunches C1, C2, and C3). In the full-grown

nymph each of these bunches is double, but for the purpose of discussing their development they are best regarded as units.

The young stages resemble the well-grown nymphs in general shape, but they have fewer gills, and below 5 mm. long bristles are present on the nota. The first instar (0·9 mm.) is white and has only three cercal and eleven antennal joints; only anal gills are present,

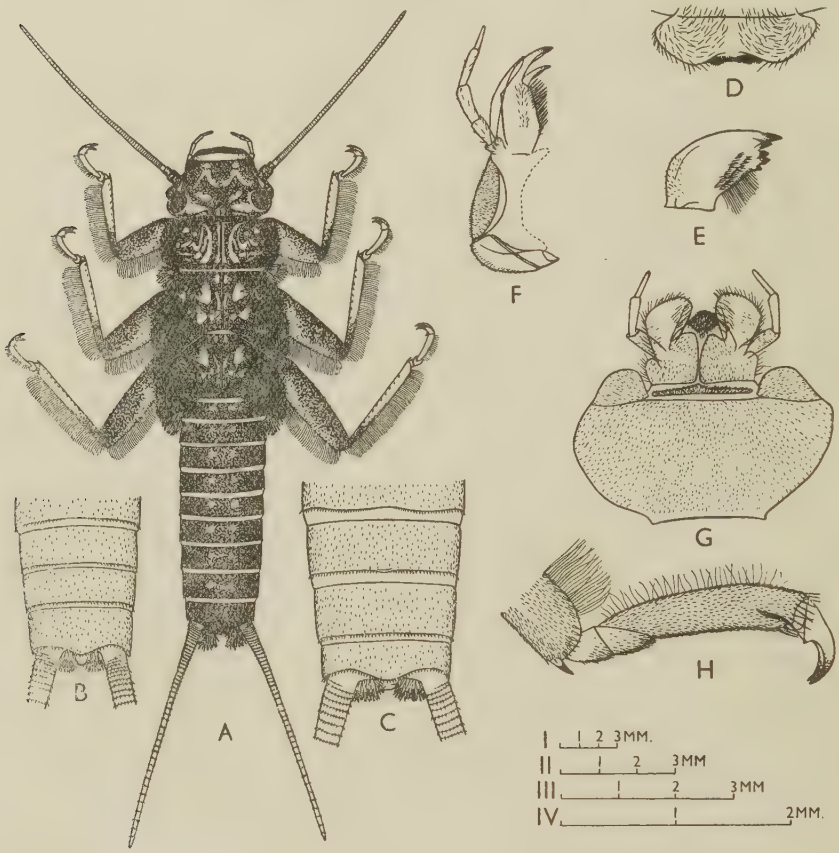

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Fig. 5.—*Perla cephalotes.* A, Full-grown female nymph (I, m); B, Tip of full-grown male abdomen in ventral view (II, m); C, Tip of full-grown female abdomen in ventral view (II, m); D, Labrum in dorsal view (III, cl); E, Right mandible in ventral view (III, cl); F, Right maxilla in ventral view (III, cl); G, Labium, with hypopharynx attached, in ventral view (III, cl); H, Hind tarsus (IV, cl).

there being four filaments, each about as long as the 10th abdominal tergum, to each sub-anal plate. At 1·5 mm. the colour is pale grey, five cercal joints are present, the anal gills are $1\frac{1}{2}$ times as long as the 10th abdominal tergum, and one filament representing gill-bunch III has appeared. At 1·75 mm. the colour is definitely grey, there are seven cercal joints, and three gill filaments in gill-bunch III. At 2·5 mm. gill-bunch III is better developed, and at 3·5 mm. gill-bunch II appears as a small boss. At this size the colour is quite dark but no pattern has appeared. At 4 mm. one or two filaments appear in gill-bunch II, and

gill-bunch I appears as a small boss. At 5 mm. the pattern begins to show vaguely, and gill-bunches I, II, and III are well developed; the anal gills remain at least as long as the 10th abdominal tergum, but now contain many filaments. At about 11 mm. gill-bunch C3 appears, and shortly afterwards C2 and C3, and these develop slowly, not attaining their full development until the nymph is about 15 mm. long. The development of the gills can be tabulated as follows :—

Length mm.	III	II	I	C3	C2	C1	Anal
0·9	—	—	—	—	—	—	+
1·5	+	—	—	—	—	—	+
3·5	+	+	—	—	—	—	+
4·0	+	+	+	—	—	—	+
11·0	+	+	+	+	—	—	+
12·0	+	+	+	+	+	—	+
14·0	+	+	+	+	+	+	+

Nymphs of this species collected in the following vice-counties have been examined : Cumberland (CU), Westmorland + N. Lancs (WL), Mid-W. Yorks (MY), S. Aberdeen (AS), and Caithness (CA).

Nymphal syntype (intermediate and dark-coloured specimens), WL, R. Brathay, 24.v.1940, full-grown nymphs (2 ♂, 3 ♀) (*Hynes*).

All the previous descriptions of this species are based entirely on colour, but they enable a reliable specific determination of specimens over about 8 mm. to be made.

Perla (*Perla* s.str.) *carlukiana* Klapálek, 1923 (fig. 6).

= *maxima* of early British lists.

Size of full-grown nymph, male 16–19 mm., female 26–33 mm.

General colour black with a bold yellow pattern above, yellow below. The markings vary to some degree in extent, and adjacent yellow areas may fuse with one another.

Head broad and flattened, with a transverse ridge behind the eyes as in *P. cephalotes*. M-line, the whole of the head in front of it, apart from the lateral edges of the frons and clypeus, and the area behind a line drawn through the posterior ocelli and the anterior margin of the compound eyes, yellow; between the ocelli is an oval yellow spot which is often fused to the pale area behind it. In dark specimens the hinder part of the vertex behind the ridge may be darkened. Antennae and mouth-parts yellow or pale grey, the labrum being dark grey to black with a more or less extensive yellow mark anteriorly. Submentum very wide and rounded at the sides.

Thorax wide and flattened, but less so than in *P. cephalotes*, the edges of the nota projecting only a short distance over the pleural gills, which are arranged as in *P. cephalotes*. Pronotum more or less rectangular, less than twice as wide as long, with a heavy black border and median line, on each side of which is a yellow area in the middle of which is a dark grey or black spot, which is usually joined by a dark streak to the anterior and posterior borders. Meso- and metanota with a black central line, which is joined on each side to the posterior inner corner of a black rectangle which lies on the side of the sclerite; the anterior margin of the notum and the outer margins of the wing pads are black, as is a line at the base of each wing pad. The wing pads of the male are somewhat smaller than those of the female.

Legs yellow, the base of the tibia darkened; a distinctive grey spot is present in the middle of the dorsal side of the femur.

Abdomen broad and slightly flattened, black above and yellow below; on each tergum,

except the first two or three in dark specimens, are two dorso-lateral yellow spots, which may fuse posteriorly on the median line, and which in very pale specimens are fused laterally to the pale area below; the 10th tergum is always yellow apart from a narrow black line anteriorly. The sexes are distinguishable as in *P. cephalotes* (p. 481) in specimens above 8 mm. Cerci as in *P. cephalotes*.

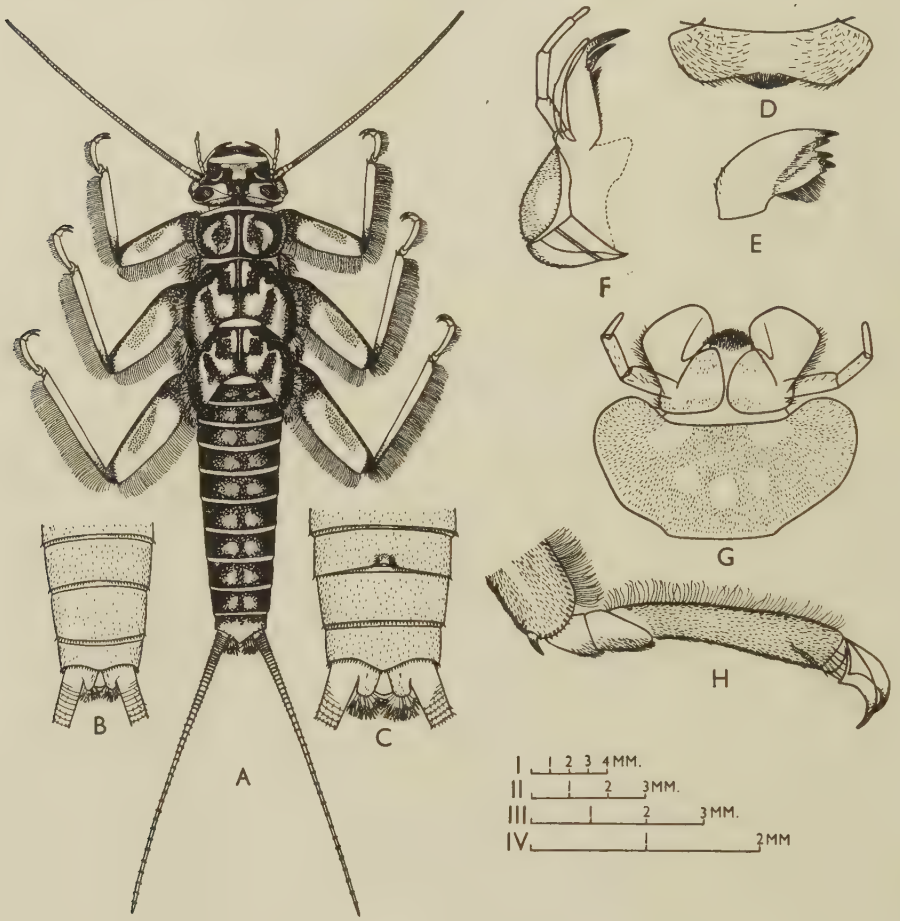

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Fig. 6.—*Perla carlukiana*. A, Full-grown female nymph (I, m); B, Tip of full-grown male abdomen in ventral view (II, m); C, Tip of full-grown female abdomen in ventral view (II, m); D, Labrum in dorsal view (III, cl); E, Left mandible in dorsal view (III, cl); F, Left maxilla in ventral view (III, cl); G, Labium, with hypopharynx attached, in ventral view (III, cl); H, Hind tarsus (IV, cl).

The young stages are less stoutly built than those of *P. cephalotes*, and, unlike the well-grown nymph, lack anal gills. The first instar (1·1 mm.), unlike that of *P. cephalotes*, has one gill filament on each side representing gill-bunch III, but apart from this the development of the pleural gills is similar to that of *P. cephalotes*. The anal gills do not appear until about 10 mm. The development of the various gill-bunches may be tabulated as follows :—

Length mm.	III	II	I	C3	C2	C1	Anal
1·1	+	—	—	—	—	—	—
1·8	+	+	—	—	—	—	—
2·5	+	+	+	—	—	—	—
5·5	+	+	+	+	—	—	—
6·0	+	+	+	+	+	—	—
7·0	+	+	+	+	+	+	—
10·0	+	+	+	+	+	+	+

The first instar is white, but at 1 mm. the colour becomes yellow, and the thoracic pattern slowly develops, appearing first as a dark margin to, and a spot on each side of, each notum. At 5 mm. the pattern can just be made out, and at 10 mm. it is fully developed.

Nymphs of this species collected in the following vice-counties have been examined: Cumberland (CU), S. Devon (SD), Westmorland + N. Lancs (WL), S. Aberdeen (AS), Caithness (CA), and Kildare (KD).

Nymphal syntypes (intermediately coloured specimens), WL, R. Rothay, 25.v.1940, full-grown nymphs (4 ♂, 4 ♀) (*Hynes*).

This species is known only from Britain, and the nymph, although it has been cited by Percival and Whitehead (1929) and figured under the name of *P. maxima* by Mosely (1921, *The Dry-Fly Fisherman's Entomology*), has not been described. The species is closely allied to *P. bipunctata* Pictet, which is the common species in Europe, and the nymph differs from that of *P. bipunctata*, as described by Schoenemund (1925a), only in that the sides of the clypeus and the part of the frons in front of the M-line are always dark, as is the outer margin of the wing pads, while in *P. bipunctata* they are yellow.

Perla (*Perla* s.str.) *marginata* Panzer, 1719.

= *maxima* (Scopoli, 1763), Schoenemund, 1925c.

Perla (*Perla*) *maxima* Scop., Klapálek 1909.
Perla (*Perla*) *marginata* Panz., Schoenemund 1925a.

According to Lucas (1932) this species was recorded from Britain by McLachlan, and there are two adult female specimens and one nymph labelled as this species in the McLachlan collection in the British Museum, but, as has already been pointed out (Hynes, 1940), these specimens are *P. carlukiana*. No other British specimens of this species have been taken, so that it seems that the name should be removed from the British list.

The nymph has been described by Schoenemund and his description should enable specimens above about 10 mm. to be recognised. The nymph as described by him and by Klapálek has no anal gills and has a thick fringe of long hairs down the inner side of each cercus. The markings are somewhat similar to those of *P. carlukiana*.

Isoperla Banks, 1906.

= *Chloroperla* Pictet, 1842.

Nymphs of this genus have been known for over a century (Pictet, 1833) and several species have since been described. It has been included in generic keys (Klapálek, 1909, Rousseau, 1921, and Uéno, 1929), but as explained above (p. 474), the characters used by these authors are not satisfactory. Kühtreiber (1934) has used in his key the shape of the sub-anal plates; a character which is much more easily seen, and reliable.

The genus is characterised by the absence of gills, the normal maxillary palp (fig. 7F), and the tooth at the base of each tarsal claw (fig. 7H). It is distinguishable from *Perlodes* and *Dictyopterygella* by the presence of clothing hairs on all parts of the body, the fringe of bristles down the inner side of the lacinia (fig. 7F), the fact that abdominal segments 1 and 2 only are divided into tergum and sternum, and by the elongate pointed sub-anal plates (fig. 7C).

Two species are listed as British (Lucas, 1932), but *I. griseipennis* is rare and very local in this country, and nymphs have not been obtained. Existing descriptions do not enable the two species to be separated reliably, and it is therefore not possible to make a key to the British species.

Isoperla grammatica (Scopoli, 1763) (fig. 7).

Perla virescens Pict., Pictet 1833 and 1842.
Chloroperla grammatica Scop., Klapálek 1909.
Chloroperla grammatica Scop., Petersen 1910.
Chloroperla grammatica Scop., Koponen 1917.
Chloroperla grammatica Scop., Kühtreiber 1934.

Size of full-grown nymph 11–16 mm., the sexes being indistinguishable.

General colour grey-green with whitish or yellowish markings above, paler below. The markings vary greatly in extent and intensity, the colour of the nymph being anything between almost uniform dark grey-green to yellow with a few dark areas. The marking is, however, always referable to a basic pattern, which is the most commonly found, and is figured here (fig. 7A).

The head is dark grey-green, usually slightly darker than the rest of the body. The clypeus is a narrow whitish membrane, and the M-line, part of the frons in front of it, a spot between the ocelli, and a spot embracing the inner margin of each compound eye, are yellow; on the vertex on each side of the epicranial suture is a small round yellow spot. All these markings may be reduced or wholly obscured, or the yellow areas may increase so much that the whole of the areas in front of the M-line and behind the posterior ocelli become yellow, giving the head a pattern similar to that described as typical of *I. griseipennis* (Kühtreiber, 1934). Specimens showing such marking have been taken on pale sandy substrata in certain southern Hampshire streams. Antennae yellow to grey, mouth-parts yellow to dark grey-green. In general structure the mouth-parts resemble those of *Dictyopterygella*, but they are covered with clothing hairs.

Thorax only slightly flattened. Pronotum elliptical with a well-marked groove, and a few short bristles round the margin; anterior and posterior margins darkened, almost black in normal specimens; lateral edges, a central longitudinal ellipse, and an L-shaped spot on each side yellow; the elliptical mark is usually darkened in the middle along the pronotal suture. These markings, like those of the head, may fuse until the condition shown in fig. 7B is reached, or the sclerite may become uniformly dark with black anterior and posterior edges. Meso- and metanota with a pattern of spots; edges of wing pads yellow. These yellow areas may increase enormously, reducing the dark areas to narrow strips, or they may be small and almost obscured.

Legs yellow, darkened at the femoro-tibial joint in well-grown intermediately coloured and dark specimens. Femur slightly flattened.

Abdomen cylindrical, grey-green above, paler below; on each tergum are two dorso-lateral yellow spots, which in the posterior segments are often fused posteriorly in the median line, making a horseshoe-shaped mark. These spots may fuse laterally with the pale areas below; or they may be absent, at least from the anterior segments. Sub-anal plates long and pointed and covered with clothing hairs. There appears to be no sexual distinction in the nymphs of this species. Cerci stout, shorter than the abdomen; each joint with a subapical whorl of stout bristles, and a dorsal fringe of long hairs.

Specimens under 5 mm. are similar to the grown nymphs in general form, but the markings are obscure or absent and the nota are covered with long bristles; black clothing hairs are present, but are few and large in proportion to the nymph. As the nymph grows the markings develop, and can be made out in intermediately coloured specimens at about 5 mm. No young specimens of light-coloured forms have been studied, but those of normally coloured specimens are light grey and darken as they grow; it is possible that the light-coloured forms show the markings at an earlier stage in their development.

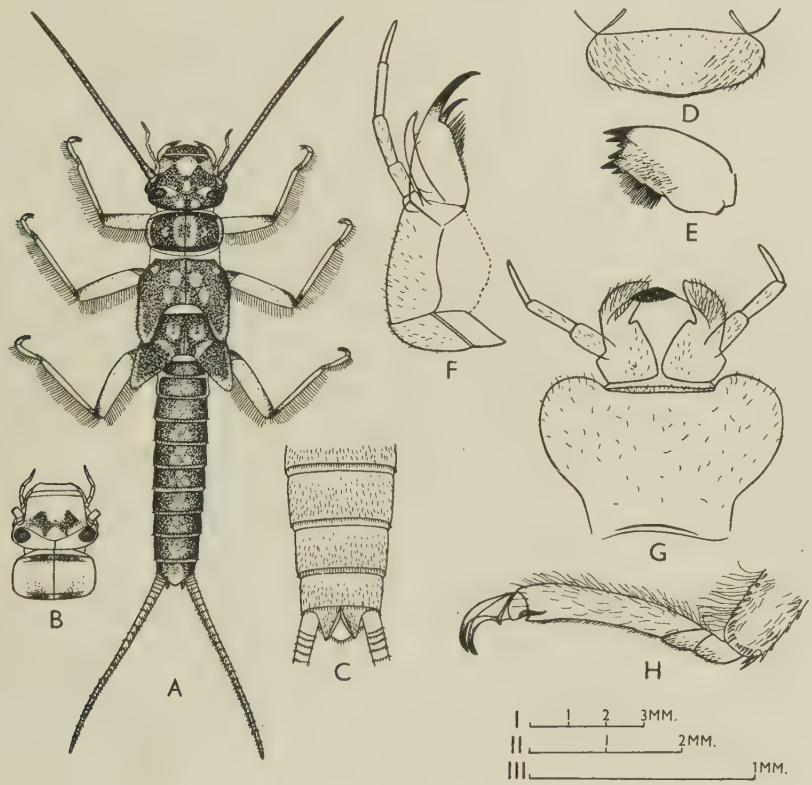

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Fig. 7.—*Isoperla grammatica.* A, Full-grown nymph (I, m); B, Head and pronotum of a light-coloured specimen (I, m); C, Tip of full-grown abdomen from below (II, m); D, Labrum in dorsal view (III, cl); E, Right mandible in dorsal view (III, cl); F, Right maxilla in ventral view (III, cl); G, Labium, with hypopharynx attached, in ventral view (III, cl); H, Hind tarsus (III, cl).

Nymphs of this species collected in the following vice-counties have been examined: Cumberland (CU), Westmorland + N. Lancs (WL), S. Hants (SH), Dorset (DT), Caithness (CA), S. Aberdeen (AS), Kildare (KD), Wicklow (WI), N. Galway (NG), and W. Donegal (WD). The very pale coloured specimens were obtained from S. Hants, Till River, 10.v.1939 (*T. T. Macan*).

Nymphal syntypes (normal coloured specimens), WL, Wray, Boathouse 2 Beck, 16.iv.1940, nymphs (17 ex.) (*Hynes*).

Earlier descriptions agree more or less with normally coloured British

specimens; and although variability in coloration has been noted by Koponen, he did not find it to be as great as is described here. Koponen and Kühtreiber have separated this species on the basis of colour, but it is possible to find specimens which do not comply with their characters.

Isoperla griseipennis (Pictet, 1842).

Chloroperla griseipennis Pict., Koponen 1917.
Chloroperla griseipennis Pict., Kühtreiber 1934.

This species is known in Britain only from the River Trent, near Nottingham, where it has been taken three times (Hynes, 1940). Two of these localities were visited in April, 1940, but no stoneflies or their nymphs were found. The Trent is now somewhat polluted, and, as Schoenemund (1925b) has pointed out, the stoneflies are usually exterminated by this. It is possible, however, that the species may have survived towards the sources of the river in the Peak District.

Neither of the existing descriptions of the species enables a specific identification to be made, although it appears from that of Koponen that the species is browner than *I. grammatica*. Kühtreiber, who gives a key to the Austrian species of the genus, states that there is no darkening at the base of the tibiae in this species, and that there is a fringe of long hairs on the cercus, while in *I. grammatica* the tibia is darkened at the base and there is no cercal fringe. As stated above, however, many British specimens of *I. grammatica* have no darkening at the tibiae, and in all well-grown nymphs there is a fringe of hairs on the cercus. Similarly Kühtreiber's figure of the head markings of *I. griseipennis* is almost identical with the markings of very pale British specimens of *I. grammatica* (fig. 7B). Koponen gives the size of the full-grown nymph of *I. griseipennis* as male 9–10 mm., female 11 mm., and states that the sexes are separable.

In the British Museum is the cast nymphal skin of an *Isoperla* collected with some adults of *I. griseipennis*, at NM. Nottingham, 3.v.1913 (*Carr*). The markings and structure of this skin are similar to those of normal *I. grammatica* nymphs, but the pronotal bristles are longer, as is described by Kühtreiber for *I. griseipennis*. This character could not, however, be used to separate the two species, because young specimens of *I. grammatica* also have long pronotal bristles.

Chloroperla Newman, 1836.

= *Isopteryx* Pictet, 1842.

Nymphs of this genus were first described by Klapálek (1909), and are easily recognised because of their small size and general proportions (fig. 8A), and the reduced fifth joint of the maxillary palp, which is only ⅓ to ¼ as wide as the fourth. There are no gills, and, unlike *Isoperla*, there is no fringe of hairs to the cerci, which are short and stout at the base, tapering rapidly towards the tip. Three species are recorded from Britain, but, as Kimmins (1936) has pointed out, the record of *C. apicalis* requires confirmation. This species is not included in the keys to the species.

Keys to the species.

Specimens over 5 mm.

1 (2). No M-line visible, only a pale spot in front of the anterior ocellus (fig. 8B). Posterior arm of the epicranial suture almost or quite absent (fig. 8B). Pronotum with an almost continuous fringe of long fine bristles round each lateral margin (fig. 8B) . . *C. torrentium* (Pict.) (p. 489).

2 (1) M-line visible as a pale line or as the boundary between a pale and dark area (fig. 8C). Posterior arm of the epicranial suture well developed, about as long as the distance from the fork to each lateral ocellus (fig. 8C). Pronotum with long fine bristles arranged in anterior and posterior groups on each side (fig. 8C) . *C. tripunctata* (Scop.) (p. 491).

Specimens 2–5 mm.

1 (2). Pronotum with an almost continuous fringe of long fine bristles round each lateral margin (fig. 8I) . . . *C. torrentium* (Pict.) (p. 489).

2 (1). Pronotum with long fine bristles arranged in anterior and posterior groups on each side, the lateral margins being glabrous (fig. 8J). (The posterior group is usually represented only by two long bristles on each side.) . . . . . *C. tripunctata* (Scop.) (p. 491).

Chloroperla torrentium (Pictet, 1842) (fig. 8 A and B and D–I).

Isopteryx torrentium Pict., Klapálek 1909.
Isopteryx torrentium Pict., Schoenemund 1927.
Isopteryx torrentium Pict., Kühtreiber 1934.

Size of full-grown nymph 7–9 mm., the sexes being indistinguishable.

General colour grey-brown with indefinite but constant markings above, yellow below.

Head slightly flattened, wider than the pronotum, smooth and shining; with one long fine bristle at each antennal base, and two or three behind each compound eye. Posterior arm of the epicranial suture reduced, the fork of the suture being almost at the posterior margin of the head. General colour grey-brown, with vaguely defined pale areas in front of the anterior ocellus, round the epicranial suture, and round each compound eye. Clypeus membranous, white or pale grey. Antennae and mouth-parts yellow, except the labrum which is dark grey-brown.

Pronotum subquadrate with a well-defined groove, and an almost or quite continuous fringe of long fine bristles round the edge. General colour grey-brown, darkened along the groove anteriorly and posteriorly. Meso- and metanota with the wing pads large and shield-shaped, alike in both sexes. Wing pads held over the back so that their inner margins are only slightly divergent in full-grown nymphs. General colour of the meso- and metanota pale, with a triangular darker mark on each side anteriorly, and a dark mark, which is less distinct distally, running down the centre of each wing pad.

Legs yellow; femora only slightly flattened; tarsal claws simple, without a tooth at the base.

Abdomen round in cross section, tapering anteriorly and posteriorly. Grey above, paler beneath. Each segment with a posterior fringe of small bristles, and a few long fine bristles. Sub-anal plates small and pointed. Sexes indistinguishable until the adult genitalia show through the cuticle shortly before emergence.

Cerci short and stout, only about $\frac{2}{3}$ the length of the abdomen. Each joint with a sub-apical whorl of short stout bristles.

As in all species of this family, the body is covered with clothing hairs, which in this genus are of the hair type.

Specimens below 5 mm. do not differ greatly from older nymphs, but the markings are less distinct, and cannot be made out in specimens below 2 mm. The posterior arm of the epicranial suture is quite absent, the anterior arms meeting on the posterior margin of the head. Ocelli appear at 4 mm. Below 2 mm. the pronotal fringe is often sparse, and the lateral margins of the sclerite may be free of bristles, making this character unreliable for separation from *C. tripunctata*. Specimens of this species below 2 mm. are not found in company with similar specimens of *C. tripunctata*, which is over 2 mm. before *C. torrentium* emerges from the egg in June or July. The first instar, which is $\frac{3}{4}$ mm. long, has three

cercal joints, and only four long pronotal bristles, two on each side of the posterior margin. The fifth joint of the maxillary palp is larger in proportion to the fourth than in older nymphs, being about $\frac{1}{2}$ the width of the fourth instead of less than $\frac{1}{3}$. It is therefore not possible on the available morphological data to distinguish this species at this early stage in its development from *C. tripunctata*, and it is difficult to place it in its genus.

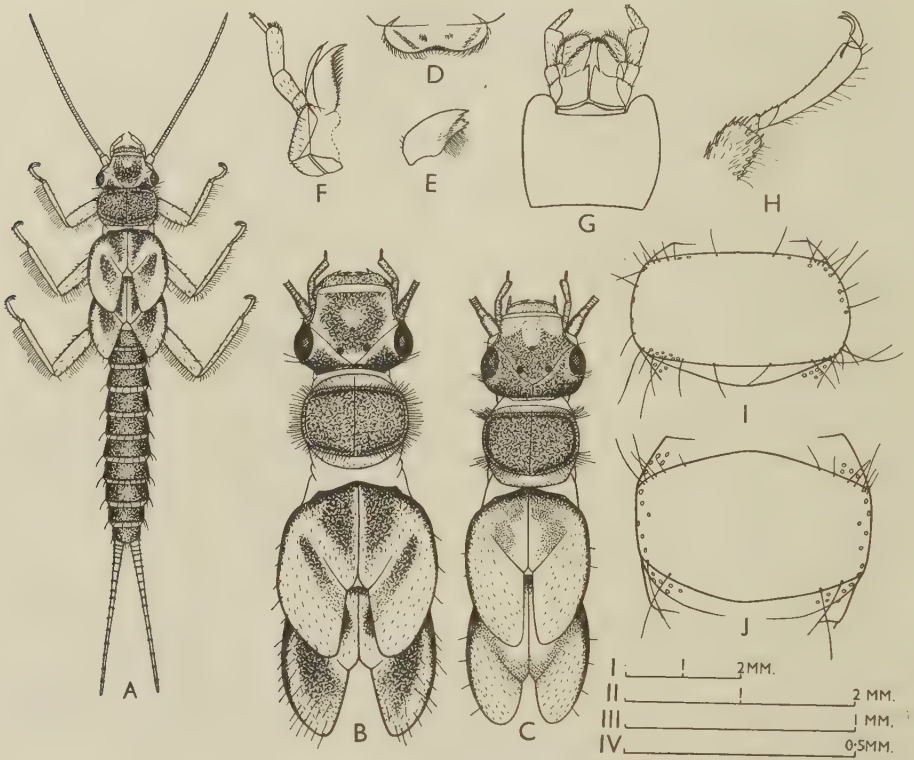

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Fig. 8.—*Chloroperla*. A, *C. torrentium*, full-grown nymph (I, s); B, *C. torrentium*, head and thorax (II, m); C, *C. tripunctata*, head and thorax (II, m); D–G, *C. torrentium* mouth-parts (III, cl): D, Labrum in dorsal view; E, Left mandible in dorsal view; F, Right maxilla in ventral view; G, Labium, with hypopharynx attached, in ventral view; H, *C. torrentium*, hind tarsus (III, cl); I, *C. torrentium*, pronotum of 3½-mm. nymph (IV, cl); J, *C. tripunctata*, pronotum of 3¾-mm. nymph (IV, cl).

Nymphs of this species collected in the following vice-counties have been examined: Cumberland (CU), Westmorland + N. Lancs (WL), S. Hants (SH), Caithness (CA), Stirling (SG), S. Aberdeen (AS), Wicklow (WI), and Kildare (KD).

Nymphal syntypes, WL, R. Rothay, 23.v.1940, full-grown nymphs (40 ex.) (*Hynes*).

Klapálek and Schoenemund both described the nymph of this species as leather-brown without marking; but, as Kühtreiber has pointed out, this is not correct. Kühtreiber has described the species at some length, and his description agrees closely with British material.

Chloroperla tripunctata (Scopoli, 1763) (figs. 8 C and J).

Isopteryx tripunctata Scop., Klapálek 1909.

Size of full-grown nymph 8·0–9·5 mm., the sexes being indistinguishable.

This species differs from *C. torrentium* as described above in the following particulars.

General colour light grey-brown with darker markings, the whole nymph being much paler than that of *C. torrentium*.

Head somewhat darker than the rest of the body, with a conspicuous yellow M-line, in front of which the frons is often entirely yellow. The area round the compound eyes and epicranial suture is slightly paler than the rest of the head. Posterior arm of the epicranial suture well developed, as long as the distance of each lateral ocellus from the fork of the suture. Labrum light grey or yellow, and unlike that of *C. torrentium*, always paler than the area of the frons between the ocelli.

Pronotum often darkened all round the groove, with long fine bristles arranged in groups on each of the anterior and posterior corners; the lateral margins of the sclerite are without bristles. The inner margins of the wing pads are subparallel in full-grown nymphs. The markings of the meso- and metanota are vague and variable, but usually consist of a slight darkening on each side of the median line and a line across the base of each wing pad.

In specimens below 4 mm. the posterior arm of the epicranial suture is absent, but it develops its full length between 4 and 5 mm. The M-line is not visible in specimens below 4·5 mm., and the other markings do not appear until 5 mm. The pronotal bristles are, however, arranged in two groups on the anterior and posterior margins of the sclerite as in the older nymphs, thus enabling the species to be distinguished from *C. torrentium*. The posterior groups of bristles usually consist of two or rarely three bristles. Specimens below 2 mm. cannot be reliably separated from *C. torrentium* on structural characters, because small nymphs of the latter species tend to have the same arrangement of bristles as *C. tripunctata* (p. 489). *C. tripunctata* nymphs are, however, about 3 mm. in June and July, when *C. torrentium* nymphs are hatching from the eggs. Accordingly specimens below 2 mm. taken before June are probably *C. tripunctata*, and specimens of this size taken during or after June are probably *C. torrentium*.

Nymphs of this species collected in the following vice-counties have been examined: Cumberland (CU), Westmorland + N. Lancs (WL), S. Aberdeen (AS), and Wicklow (WI).

Nymphal syntypes, WL, R. Rothay, 6.v.1939, full-grown nymphs (4 ex.) (*Hynes*).

Klapálek's brief description of the nymph does not entirely agree with British material, for he describes the head as distinctly narrower than the pronotum, while in all the specimens examined the head is as wide as, or wider than, the pronotum. He also uses the shape of the pronotum as the specific character, but, as can be seen by comparing figs. 8C and 8J, this varies with age. Further, he gives the number of cercal joints as a specific character. This latter character and several similar characters involving the proportionate lengths and breadths of cercal joints and the length of bristles have often been used in the specific separation of nymphs, but all are rendered invalid by the fact that, as is pointed out by Wu (1923), these proportions change radically with age. The exact extent of such changes and their relationship to the age and instar are quite unknown. Similarly Kühtreiber (1934) has shown that in a regenerating cercus the proportions are different from the normal condition; regenerating cerci are frequently found in nature.

Chloroperla apicalis Newman, 1836.

Isopteryx apicalis Newm., Schoenemund 1927.

Newman recorded this species from Britain, and his specimens, which are adult females, are in the Hope Department of Entomology, University Museum, Oxford. The species has, however, not been recorded since, and Kimmins (1936) has suggested that the record requires confirmation. The nymph is mentioned by Schoenemund, who says it is yellow. No other description has been published.

6. Taeniopterygidae Klapálek, 1909.

The nymph of one species belonging to this family was first described by Pictet (1832), and since then several European species belonging to three separate genera have been described. Lestage (Rousseau, 1921) first included the family in a key to the nymphs.

The family is characterised by the well-developed glossae (figs. 9H and 10H), the labrum which is less than twice as wide as long (figs. 9D and 10D), the reduced 10th abdominal sternum (fig. 9C), the fact that each joint of the tarsus is longer than the preceding joint (figs. 9I and 10I), and the simple tarsal claws. All species of the family apparently have long antennae and cerci, and the wing pads are held obliquely to the body. Retractile coxal gills are present in *Taeniopteryx* (fig. 9B), and *Brachyptera* and *Rhabdiopteryx* (Kühtreiber, 1934) have a small pit at the tip of each antennal joint in which lie sensillae (fig. 2B).

Three genera are recorded from Britain, all of which have been included together in a generic key by Kühtreiber (1934). As, however, there is some doubt as to the validity in this country of the characters on which he separates *Brachyptera* and *Rhabdiopteryx*, and as the latter has only once been recorded in Britain, it is not included in the generic key.

Taeniopteryx Pictet, 1842.

= *Nephelopteryx* Klapálek, 1902.

Nymphs of this genus have been known since the beginning of the century (Lauterborn, 1903) and have often been described since. Two species are known, *T. nebulosa* (L.) and *T. schoenemundi* Mert., but there is some doubt as to the validity of the characters which have been used in their separation (Mertens, 1929, and Kühtreiber, 1934).

The genus is characterised by the presence of an apparently three-segmented retractile gill on the inner side of each of the coxae (fig. 9B), and by the presence of median spines on the hind margin of each abdominal tergum.

One species only is recorded from Britain (Lucas, 1932).

Taeniopteryx nebulosa (Linnaeus, 1766) (fig. 9).

Taeniopteryx nebulosa L., Lauterborn 1903.
Nephelopteryx nebulosa L., Klapálek 1909.
Nephelopteryx nebulosa L., Petersen 1910.
Nephelopteryx nebulosa L., Lestage 1921.
Nephelopteryx nebulosa L., Rousseau 1921.
Nephelopteryx nebulosa L., Schoenemund 1927.
Nephelopteryx nebulosa L., Kühtreiber 1934.

The following description, which agrees closely with the previous descriptions of the species in Europe, is based on only three full-grown females and a few first instar nymphs.

Size of full-grown female nymph 12 mm., the male is probably slightly smaller.

General colour dark grey-brown with vague darker markings above, paler below.

Head rounded, as wide as the pronotum, uniformly dark grey-brown. Ocelli in an equilateral triangle. Antennae long, scape large and prominent. Lestage states that he

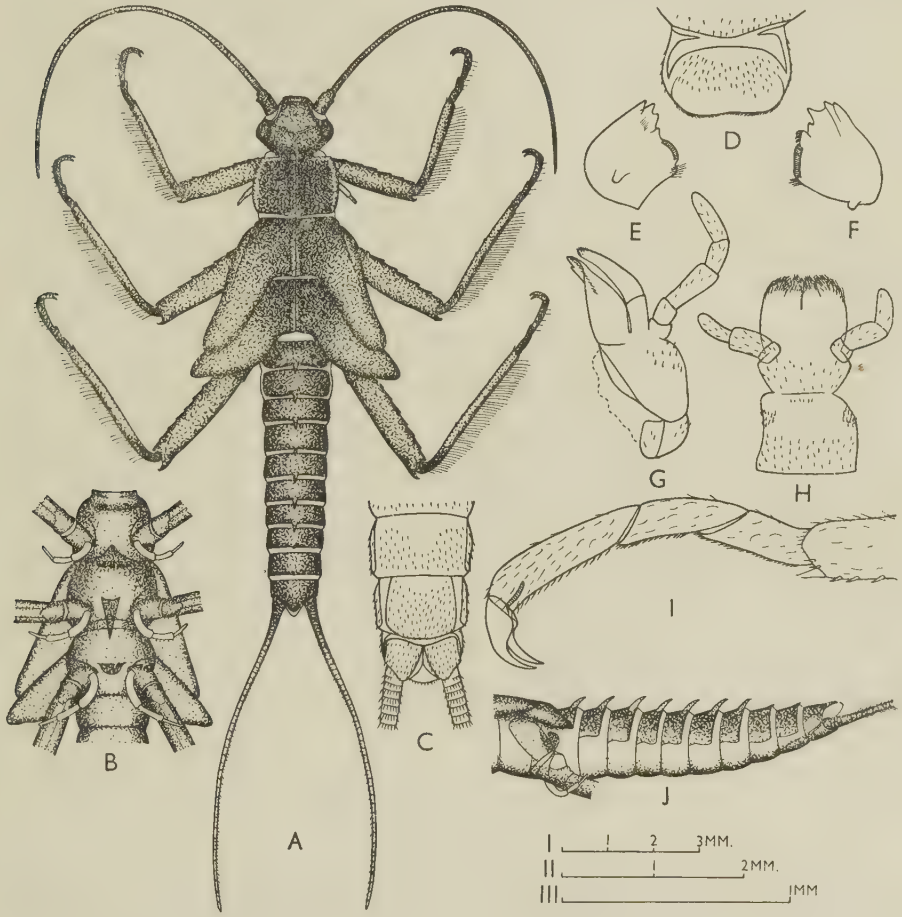

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Fig. 9.—*Taeniopteryx nebulosa.* A, Full-grown female nymph (I, m); B, Thorax of full-grown nymph in ventral view (I, m); C, Tip of full-grown female abdomen in ventral view (II, m); D, Labrum in dorsal view (III, cl); E, Right mandible in ventral view (III, cl); F, Left mandible in ventral view (III, cl); G, Left maxilla in ventral view (III, cl); H, Labium in ventral view (III, cl); I, Hind tarsus (III, cl); J, Full-grown female abdomen in lateral view (I, m).

can find no trace of the fine bristles covering the maxillary palp as figured by Klapálek. These can be seen in the three full-grown British specimens, but are not nymphal structures, being present on the underlying cuticle of the adult palp, which can be removed by dissection. Such structures can often be seen through the cuticle of full-grown nymphs. There are a few scattered hairs on the mouth-parts, which are well developed.

Pronotum quadrate, wider than long, conspicuously ridged down the middle, and drawn into an upwardly directed blunt point anteriorly and posteriorly. This sclerite is slightly paler on the lateral margins and Lestage figures a dark oval area on each side of the median ridge, which is not present in the British specimens. Meso- and metanota with a median ridge as in the pronotum, and darkened laterally. Wing pads large and pale; in the male, the adult of which is brachypterous, the wing pads are probably less prominent.

Legs long, grey-brown. Each coxa with an apparently 3-segmented retractile tracheal gill on the inner side. Femora more or less circular in cross section, and grooved anteriorly; on each side of this groove is a serrated ridge. Tibiae and tarsi with a sparse fringe of long hairs posteriorly. Tarsi long, claws simple.

Abdomen cylindrical; sterna 1–8 undeveloped; terga 1–7 each with a stout median upwardly directed spine on the hind margin. Similar but much smaller spines are present on terga 8 and 9. The number of segments on which these spines occur has been used as a specific character, but it appears (Mertens, 1929, and Kühtreiber) that this is somewhat variable. The 10th tergum is drawn out posteriorly. In the female the 9th sternum is chitinised and the sub-anal plates are wide and bluntly pointed. Lestage says that in the male the 9th sternum is drawn out posteriorly, and that there is a prominent lobe, the supra-anal lobe of the adult, on the hind margin of the 10th tergum.

Cerci pale brown, long, each joint with a distal whorl of small bristles, and with a sparse fringe of hairs dorsally and ventrally.

This species is covered with small fine bristles, which may be regarded as clothing hairs. Stouter bristles occur at the tip of each serration on the femora, and sparsely on the tibiae.

The young stages appear from the previous descriptions to be similar to the older nymphs, but it is possible that such features as the abdominal spines, which Lestage says are less developed in smaller specimens, and the serrations on the tibiae, are absent; both gills and abdominal spines are absent from the first instar, which greatly resembles the NEMOURIDAE.

Nymphs of the species collected in only one locality in Westmorland + N. Lancs (WL) have been examined.

Nymphal type, WL, Dyke near River Winster at Helton Tarn, 28.ii.1939, full-grown nymph (♀) (*T. T. Macan*).

Brachyptera Newport, 1851.

= *Taeniopteryx* Pictet, 1842.

Pictet (1833) first described the nymph of a species now placed in this genus, and several other European species have since been described, but it is doubtful how far these descriptions, with the exception of those of *B. trifasciata* (Pict.) and *B. seticornis* (Klap.) (Kühtreiber, 1934), enable specific identification to be made.

The genus is separated from *Taeniopteryx* by the absence of coxal gills and dorsal abdominal spines, and the posterior elongation of the 9th abdominal sternum (fig. 10 B and C), and Kühtreiber has separated it from *Rhabdiopteryx* on the shape of the epicranial suture. Unfortunately, this character does not hold in Britain. Kühtreiber states that in *Rhabdiopteryx* the angle between the two arms of the epicranial suture is approximately 120 degrees, while in *Brachyptera* it is much more; in British *B. risi* this angle is almost exactly 120 degrees (fig. 10J). The full-grown nymphs of these two genera may, however, be separable on the developing genitalia. In the male nymph of *Brachyptera* the sub-anal plates are drawn out into sharp hooks, and the hind end of the 9th sternum is rounded, while in *Rhabdiopteryx*, as described by

Kühtreiber, the sub-anal plates are drawn out into blunt points and the hind margin of the 9th sternum is truncated. In the female, which is easily distinguished from the male in both genera by the simple sub-anal plates, the hind margin of the 9th sternum is drawn out into a blunt point in *Brachyptera* and is simply rounded in *Rhabdiopteryx*. This character should, however, be regarded with suspicion in Britain, because it seems probable that the *Rhabdiopteryx* recorded here is new to science (Hynes, 1940), and the nymph of *B. putata* is unknown.

Two species of the genus are recorded from Britain (Morton, 1911), the nymph of only one of which is known.

Brachyptera risi (Morton, 1896) (fig. 10).

Taeniopteryx risi Mort., Mertens 1921 and 1923.

Size of full-grown nymph 7–10 mm., there being no marked difference in size between the sexes.

General colour grey or red-brown, yellow or reddish below; appendages grey to yellow.

Head rounded, brown. Ocelli in an isosceles triangle. In front of the anterior ocellus is a U-shaped mark representing the two inner sectors of the M-line. Dorsal callosities triangular. On the vertex of many specimens there is a vague mottling of darker brown. Antennae long and glabrous, with a large prominent scape. Mouth-parts yellow, similar to those of all the Filipalpia except that the tip of the galea is drawn out into a point, on the outer side of which is a complex comb of fine curved bristles (fig. 2D).

Pronotum trapezoidal, widest behind, slightly longer than wide, and membranous anteriorly. A few darker marks are often present on each side of the suture, which together make up a dark oval area on each side, similar to that described and figured in *Taeniopteryx* by Lestage (1921). Meso- and metanota dark coloured, with a pale median line, particularly posteriorly, and a vague paler mark on each side anteriorly. Wing pads pale, equally developed in both sexes.

Legs grey to yellow, stout. Femur more or less circular in cross section and grooved anteriorly to receive the cylindrical tibia. Tarsi darkened. Femur, tibia and tarsus with a fringe of hairs posteriorly.

Abdomen cylindrical; sterna 1–7 in the female, and 1–8 in the male, membranous. Terga about three and a half times as wide as long. 10th tergum drawn out posteriorly into a blunt point; all the terga are grey-brown, the 10th having two small pale dorso-lateral spots on the anterior margin. In the female the 8th sternum is lightly chitinised and T-shaped, and the 9th is drawn out backwards into a blunt point; the sub-anal plates, which are completely covered by the 9th sternum, are simple. In the male the 8th sternum is membranous, and the 9th is drawn out backwards and rounded at the end; the sub-anal plates are drawn out into sharp heavily chitinised hooks, which project from under the 9th sternum. The sexes are distinguishable above 4 mm. Cerci long, yellow and darkened at the tip; each joint bearing an apical ring of very small bristles.

The young nymphs resemble the well-grown nymphs in most particulars. At 1·5 mm. the colour is uniform grey above and yellow below, and the 9th sternum is unmodified. At 2 mm. the 9th sternum begins to be drawn out backwards, and at 3 mm. it is fully developed. Between 3 and 4 mm. the ocelli and markings appear, and the 9th sternum becomes the shape characteristic of the sex of the nymph. In the male the sub-anal plates become drawn out backwards into outwardly curved lobes, which become sharp-pointed hooks at about 5 mm.

As in *Taeniopteryx*, sparse clothing hairs are present, and bristles occur only on the tibiae.

Nymphs of this species collected in the following vice-counties have been examined : Cumberland (CU), Westmorland + N. Lancs (WL), and S. Hants (SH); and specimens from many localities in Ireland, probably of this species, have been seen.

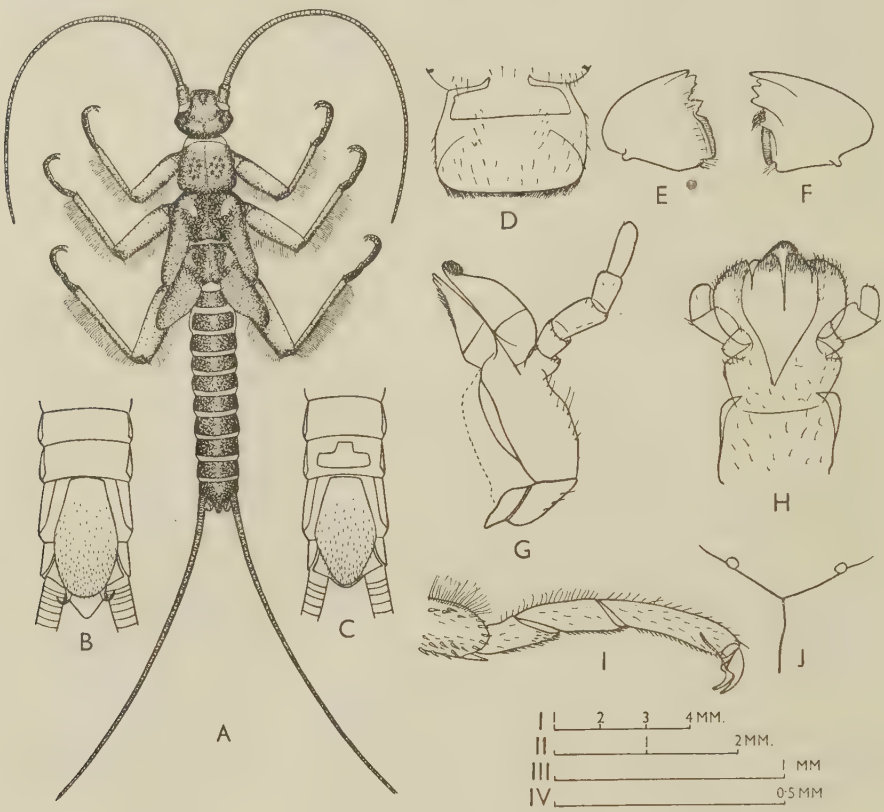

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Fig. 10.—*Brachyptera risi*. A, Full-grown male nymph (I, m); B, Tip of full-grown male abdomen in ventral view (II, m); C, Tip of full-grown female abdomen in ventral view (II, m); D, Labrum in dorsal view (IV, cl); E, Right mandible in ventral view (IV, cl); F, Left mandible in ventral view (IV, cl); G, Left maxilla in ventral view (IV, cl); H, Labium, with hypopharynx attached, in ventral view (IV, cl); I, Hind tarsus (III, cl); J, Epicranial suture (III, cl).

Nymphal syntype, WL, Wray, Boathouse 2 Beck, 15.ii.1939, full-grown nymphs (2 ♂, 2 ♀) (*Hynes*).

Full-grown nymphs of this species may be separated from the European species *B. trifasciata* (Pict.) and *B. seticornis* (Klap.) as described by Kühtreiber (1934) as follows :—

1. Head with a U-shaped mark in front of the anterior ocellus. Pronotum trapezoidal. Abdominal terga $3\frac{1}{2}$ times as wide as long. 10th tergum with two pale spots on the anterior margin. 9th sternum rounded at the tip in the male (length : breadth = 12 : 7), pointed at the tip in the female (length : breadth = 2 : 3). . . . . *B. risi.*

2. Head with an X-shaped darker mark. Pronotum almost parallel-sided. Abdominal terga at most 3 times as wide as long. 10th tergum unicolorous. 9th sternum pointed at the tip in both sexes (length : breadth = 2 or 3 : 1) . . . . . *B. trifasciata.*
3. Head uniformly brown. Pronotum trapezoidal. Abdominal terga 3 or 4 times as wide as long. 10th tergum with two pale spots on the anterior margin. 9th sternum rounded at the tip in both sexes, and less than twice as wide as long . . . . . *B. seticornis.*

From *T. braueri* Klap. as described and figured by Klapálek (1909) it is inseparable. The description of the species as given above is in close agreement with the less detailed descriptions of Mertens.

Brachyptera putata (Newman, 1838).

The nymph of this species, which is recorded in Britain only from Scotland, is unknown.

Rhabdiopteryx Klapálek, 1902.

The nymph of *R. neglecta* (Albarda) 1889 has been described by Kühtreiber (1931) and later (1934) was included by him in a key, but, as is explained above (p. 494), the characters proposed by him are not valid in Britain. Furthermore, there is some doubt as to whether the one British specimen of this genus belongs to this species (Hynes, 1940). It is therefore not possible to give any characters by which this genus may be recognised in Britain.

The one British specimen, which has been doubtfully referred to *R. neglecta*, was from Yorks, Harwood Dale, Jugger Beck, 10.iv.1927 (♀) (*Whitehead*).

7. Capniidae Klapálek, 1909.

The nymph of *Capnia nigra* was first described by Pictet (1842) and has been described several times since. Nymphs of only one other European species of the family, *C. conica* Klap. (Kühtreiber, 1931 and 1934), are known at present. The family has been placed in a family key to the nymphs by Lestage (Rousseau, 1921), who based his key on the generic key given by Klapálek (1909). The characters given, which have also been used by Kühtreiber (1934), are the proportions of length to width of the glossae and sub-anal plates. Lestage has also stated erroneously that the first two tarsal joints are subequal, whereas in the Leuctridae they are not; his figure of the tarsus of *Capnia* shows the second joint as shorter than the first, which agrees with what has been observed in British material. The differences in proportion of the length to width of the glossae which are claimed to separate the Capniidae and Leuctridae do not exist in Britain, where the glossae of *Leuctra* are certainly longer than wide (fig. 12H), as in *Capnia*. A hitherto undescribed abdominal character is therefore proposed for the separation of these two families. It is possible that it will not apply to the two species of *Capnia* which are recorded from Britain but whose nymphs are unknown, but this seems unlikely because it can be used to separate the North American species *Allocapnia pygmaea* Burm. from European and American species of *Leuctra*, and some Capniidae nymphs collected in Tibet: Everest Base Camp, Rongbuk Glacier, 16,500 ft., v.1922 (*T. G. Longstaff*), show the same character. Also, Kühtreiber (1931) has given figures of the abdomen of the nymph of *C. conica* which indicate that the same structure is present in that species. It would seem, therefore, that some reliance can be placed in this easily seen character for the separation of these two families.

Similarly, a character involving the relative lengths of the hind legs and abdomen is proposed for the separation of the CAPNIIDAE and LEUCTRIDAE from the NEMOURIDAE. This applies to all the European and American material which has been examined, and is easier to see than the characters given by Lestage.

The family is characterised by the fully developed glossae which are longer than wide (fig. 11H), the labrum which is subquadrate and less than twice as wide as long (fig. 11D), the reduced 10th abdominal sternum (fig. 11 B and C), the proportions of the tarsal joints, the 2nd of which is shorter than the 1st (fig. 11I), the wing pads held more or less parallel to the body (fig. 1B), the division of abdominal segments 1–9 into tergum and sternum (fig. 1C), the sub-anal plates which are wider than long (fig. 11 B and C), and the fact that the hind leg when stretched back alongside the abdomen does not reach beyond its tip.

One genus, the only European genus of which the nymphs are known, is listed as British (Lucas, 1932).

Capnia Pictet, 1842.

The generic characters are those given above for the family. The nymphs of only two European species are known, *C. nigra* first described by Pictet (1842) and described many times since, and *C. conica* Klap. described by Kühtreiber (1931).

Three species are listed as British (Morton, 1929), the nymphs of one only being known.

Capnia nigra Pictet, 1842 (fig. 11).

Perla (*Capnia*) *nigra* Pictet, 1842.
Capnia nigra Pict., Klapálek 1909.
Capnia nigra Pict., Petersen 1910.
Capnia nigra Pict., Randers 1915.
Capnia nigra Pict., Schoenemund 1927.

Size of full-grown nymph, male 6–8 mm., female 7–9 mm.

General colour yellow to brown above, yellow below; with yellow appendages.

Head rounded, wider than the pronotum, often slightly darker than the rest of the body. Ocelli and eyes dark brown. Dorsal callosities elliptical. The distance between the posterior ocelli is less than twice the distance of each from the inner margin of the compound eye. Antennae and mouth-parts typical of the Filipalpia, except that the mentum is larger than in some forms.

Pronotum trapezoidal, wider behind; brown but paler in the middle. Meso- and metanota similarly coloured. In the male the wing pads are so reduced that they do not even reach to the hind margin of the notum (fig. 11A); in the female they are normal (fig. 1B).

Legs stout, hind femur about four times as long as wide, and more or less round in cross section. Femur, tibia and tarsus with a fringe of fine hairs posteriorly.

Abdomen uniformly yellow-brown above, and yellow below. In the male the 10th tergum is drawn out backwards into a blunt point, and in the female it is rounded. This enables the sex of specimens over 5 mm. to be determined. Cerci about as long as the abdomen; each joint bearing a whorl of stout bristles at the tip.

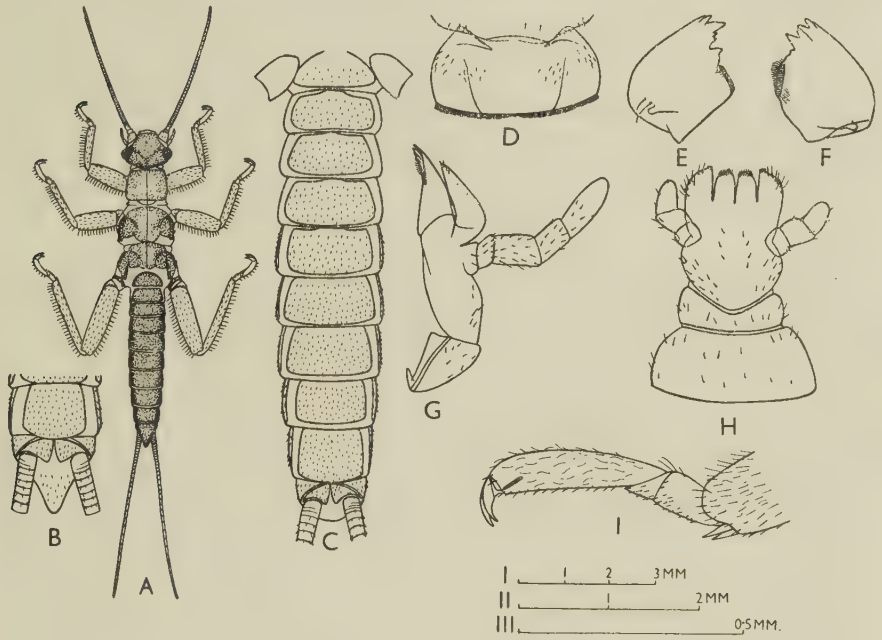
The legs and abdomen are covered with clothing hairs, and few bristles are present.

The young stages differ from the full-grown nymphs only in their paler colour, the lack of wing pads and the absence of the posterior prolongation of the 10th tergum in the male.

Nymphs of this species collected only in Westmorland + N. Lancs (WL) have been examined.

Nymphal syntypes, WL, Windermere, 9.iv.1940, full-grown nymphs (2 ♂, 2 ♀) (*Hynes*).

Previous descriptions of this species do not enable it to be separated from the European species *C. conica* Klap. (Kühtreiber, 1931), but it seems that they are easily separated on the galea, the tip of which is simple in *C. nigra* (fig. 11G) and which is described and figured as bifid in *C. conica* by Kühtreiber.



II

Fig. 11.—*Capnia nigra.* A, Full-grown male nymph (I, s); B, Tip of full-grown male abdomen in ventral view (II, s); C, Female abdomen in ventral view (II, s); D, Labrum in dorsal view (III, cl); E, Right mandible in ventral view (III, cl); F, Lef mandible in ventral view (III, cl); G, Left maxilla in ventral view (III, cl); H, Labium in ventral view (III, cl); I, Hind tarsus (III, cl).

Capnia vidua Klapálek, 1906.

The nymph of this species is unknown, but adults have been recorded from many places in Britain.

Capnia atra Morton, 1896.

The nymph of this species is unknown, but adults have been recorded from Scotland and Ireland. It differs from both the previous species in that the adult male is fully winged, and this fact should enable the full-grown male nymphs to be recognised.

8. Leuctridae Klapálek, 1909

The nymphs of several species of the one European genus of this family are known, and the genus has been included in keys by several authors (Klapálek,

1909, Rousseau, 1921, and Kühtreiber, 1934). As explained above (p. 497), however, the characters used are not satisfactory for the separation of this family from the CAPNIIDAE, and new ones have been proposed and found reliable in European and American material.

The family is characterised by the well-developed glossae (fig. 12H), the subquadrate labrum, which is less than twice as wide as long (fig. 12D), the reduced 10th abdominal sternum (fig. 12J), the proportions of the tarsal joints, the second of which is shorter than the first (fig. 12I), the wing pads held more or less parallel to the body (fig. 12 A–C), the division of abdominal segments 1–4 only into tergum and sternum (fig. 12J), the sub-anal plates which are longer than wide (fig. 12J), and the fact that the hind leg when stretched back alongside the abdomen does not reach beyond its tip.

There is only one European genus of this family, and it is recorded from Britain.

Leuctra Stephens, 1836.

The generic characters are those given above for the family. Nymphs of the genus were first described by Klapálek (1909), and several species have since been described. Kühtreiber (1934) has made a key to the nymphs of several Austrian species.

All the known European nymphs of the genus are slender cylindrical pale coloured nymphs with well-developed wing pads, which are not much reduced even in the nymphs of the brachypterous forms found at high altitudes (p. 548). The mouth-parts of all the six British species are similar, and typical of the Filipalpia; the glossae, as stated above, are longer than wide. Lestage (1920) has described sexual differences in the nymphs of *L. geniculata*, but these have not been seen in British specimens of the species, nor have any sexual differences been observed in the other five British species.

Six species of the genus occur in Britain (Mosely, 1932), the nymphs of four of which are very alike, and can only be separated morphologically on the arrangement of bristles and clothing hairs, often involving the use of great magnification. Identification is, however, made much easier if the size of the nymph together with the date of the capture are taken into account, because, of these four species, two, *L. hippopus* and *L. inermis*, emerge as adults in the spring and early summer, and two, *L. fusciventris* and *L. moselyi*, emerge in the late summer and autumn. Accordingly, in the following keys to the species, use has been made of the size of the nymphs and the month of capture, and these are used as major characters in some places in the keys. It must be emphasised, however, that these keys are based on observations made almost entirely in the Lake District, and that variations may occur in other parts of the country. The emergence period of the adults seems, however, to be consistent throughout the country (Hynes, 1940) and nymphs sent from other parts of the country for identification have always agreed with those from the Lake District.

Keys to species.

Specimens over 5 mm.

1 (2). Nymph with broad flattened head bearing stout curved antennae, the basal segments of which bear chitinous projections and long bristles (figs. 12A and 13K) . . . . *L. geniculata* Steph. (p. 501).

2 (1). Nymph with rounded head bearing slender straight antennae (figs. 12 B and C and 13L).

3 (4). Pronotum with a thick fringe of long fine hairs (fig. 13D). Similar hairs on most parts of the body (fig. 12B). General colour orange-yellow . . . . . *L. nigra* (Oliv.) (p. 503).

4 (3). Pronotum with a few bristles laterally and antero-laterally (fig. 13 E and F). A few fine bristles on the rest of the body (fig. 12C). General colour grey-brown.

5 (6). Tibiae of all legs with a fringe of long fine hairs on the posterior margin (fig. 13G) . . . . . *L. fusciventris* Steph. (p. 505).

6 (5). Tibiae of all legs with only a few scattered fine hairs on the posterior margin, not forming a fringe (fig. 13H).

7 (8). Abdominal terga 2–10 each with at least one pair of long dorso-lateral bristles (fig. 13A) . . . . . *L. inermis* Kemp. (p. 503).

8 (7). Abdominal terga 1–4 without long dorso-lateral bristles (fig. 13 B and C); these may, however, be present on the more posterior segments.

9(10). Specimens taken between October and May inclusive. More than 12 bristles on each side of the pronotum (fig. 13E). Clothing hairs present on abdominal tergum 2 and usually also on tergum 1 (fig. 13B) . . . . . *L. hippopus* Kemp. (p. 505).

10 (9). Specimens taken between May and August inclusive. Less than 12 bristles on each side of the pronotum (fig. 13F). No clothing hairs present on abdominal terga 1 and 2 (fig. 13C). *L. moselyi* Mort. (p. 506).

Specimens 2–5 mm.

1 (4). Pronotum with a fringe of long fine hairs (fig. 13D).

2 (3). Specimens taken between late April and June inclusive. Head broad and flattened in larger specimens (fig. 12A). Antennae slightly curved and bearing long bristles in the basal segments. (Living in deep running water with a clean stony substratum.) *L. geniculata* Steph. (p. 501).

3 (2). Specimens taken between August and early April inclusive. Head rounded (fig. 12B). Antennae slender and straight (fig. 12B), occasionally with a few scattered hairs on the basal segments. (Living in stony but slightly silted localities.) *L. nigra* (Oliv.) (p. 503).

4 (1). Pronotum with a few scattered bristles laterally (fig. 13 E and F).

5 (6). Abdominal terga 2–10 each with at least one pair of long dorso-lateral bristles (fig. 13A). (Specimens taken between September and April inclusive.) . . . . . *L. inermis* Kemp. (p. 503)

6 (5). Abdominal terga 1–4 without long dorso-lateral bristles (fig. 13 B and C); these may, however, be present on the more posterior segments.

7 (8). Specimens taken between September and December inclusive. *L. hippopus* Kemp. (p. 505).

8 (7). Specimens taken between March and August inclusive.

9(10). Metanotum with a few conspicuous fronto-lateral bristles (fig. 13I). Pronotum usually with 12 or more bristles on each side (as fig. 13E) *L. fusciventris* Steph. (p. 505).

10 (9). Metanotum without conspicuous fronto-lateral bristles (fig. 13J) (one or two very small ones are very occasionally present). Pronotum with fewer than 12 bristles on each side (fig. 13F) *L. moselyi* Mort. (p. 506).

Leuctra geniculata Stephens, 1836 (figs. 12A and 13K).

Leuctra geniculata Steph., Lestage 1920.

Size of full-grown nymph 8–11 mm.

General colour light grey-brown above with yellow wing pads, and yellow below; appendages yellow.

Head wider than long, and flattened, with a ridge between the bases of the antennae in front of which the frons narrows rapidly. Ocelli clearly defined. Antennae long and curved, scape large and stout. The joints of the basal third of the flagellum are modified,

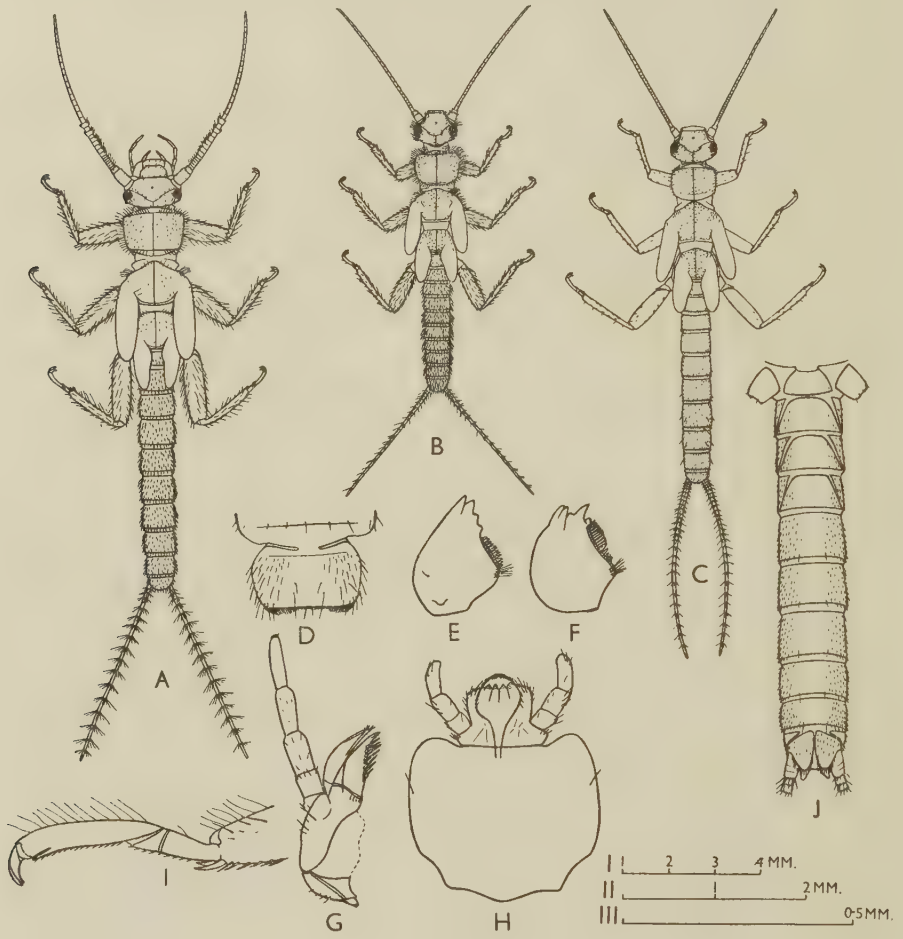


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Fig. 12.—*Leuctra*. A, *L. geniculata*, full-grown nymph (I, s); B, *L. nigra*, full-grown nymph (I, s); C, *L. hippopus*, full-grown nymph (I, s); D–H, *L. fusciventris*, mouth-parts (III, cl): D, Labrum in dorsal view; E, Right mandible in ventral view; F, Left mandible in dorsal view; G, Right maxilla in ventral view; H, Labium, with hypopharynx attached, in ventral view; I, *L. fusciventris*, hind tarsus (III, cl); J, *L. hippopus*, full-grown abdomen in ventral view (II, s).

several of the more proximal joints bearing chitinised lobes on the anterior margin; these are followed by a variable number of joints bearing similar projections both anteriorly and posteriorly, and alternating with normal joints; all the joints in the region thus modified bear long fine bristles. The mandibles are larger in proportion to the other mouth-parts than in the other species of the genus.

Pronotum trapezoidal, wider than long.

The whole of the body, except for the centres of the nota and the wing pads, is covered with long fine hairs, some of which form a well-developed fringe to the pronotum. There is a long somewhat stouter bristle on each sub-anal plate, and each cercal joint has a distal whorl of long bristles.

The young stages differ somewhat from the full-grown nymphs. At 2 mm. the head is rounded, and the antennae are only slightly curved and without projections, although the long bristles are present on the basal joints. The ocelli appear at 4 mm., and between 4 and 5 mm. the head assumes its characteristic shape. Above 5 mm. the antennal projections begin to appear, those in the middle of the proximal series being the first to develop. The anterior and posterior projections on the more distal segments appear a little later, and increase in size and number throughout the life of the nymph; as many as five sets may develop.

Nymphs of this species collected in the following vice-counties have been examined: Cumberland (CU), Westmorland + N. Lancs (WL), S. Hants (SH), and S. Aberdeen (AS).

Nymphal syntypes, WL, R. Rothay, 23.viii.1939, full-grown nymphs (4 ex.) (*Hynes*).

This species grows rapidly during the early summer, and the adults emerge in late summer and autumn.

Leuctra nigra (Olivier, 1811) (figs. 12B and 13D).

= *nigra* Pictet, 1842.

Leuctra nigra Pict., Klapálek 1909.
Leuctra nigra Pict., Kühtreiber 1934.

Size of full-grown nymph 6–7 mm.

General colour orange-yellow above with yellow wing pads, and paler below; appendages yellow.

Head rounded; antennae slender and straight, often with a few scattered fine hairs on the basal joints. Ocelli black and clearly defined.

The entire body, except the centres of the nota and the wing pads, is covered with long fine hairs, some of which form a well-developed fringe to the pronotum. Each cercal joint has a distal whorl of long bristles.

The young stages are similar to the grown nymphs, and differ only in that ocelli are absent in specimens below 4 mm.

Nymphs of this species collected in the following vice-counties have been examined: Westmorland + N. Lancs (WL), Cumberland (CU), and Dublin (DU).

Nymphal syntypes, WL, Wray, Boathouse 2 Beck, 21.v.1940, full-grown nymphs (15 ex.) (*Hynes*).

This species grows during the winter and early spring, and adults emerge in the spring and early summer.

Leuctra inermis Kempny, 1899 (fig. 13A).

Leuctra inermis Kemp., Kühtreiber 1934.

Size of full-grown nymph 6–8 mm.

General colour brown above, somewhat darker than the other British species, with paler wing pads, and pale brown below; appendages yellowish.

Head rounded; antennae slender and straight. A few bristles behind the eyes and one at the base of each antenna. Ocelli black and well defined.

Pronotum quadrate, wider than long, with about 12 bristles on each lateral margin. Meso- and metanota with a few antero-lateral bristles.

Legs with scattered bristles and one or two long hairs on the posterior margin of the tibia.

Abdominal terga covered with fine clothing hairs. Terga 2–10 each with a pair of long dorso-lateral bristles about half-way down its length, and on terga 5–10 there is a varying number of more lateral pairs of similar bristles. Cerci with an apical fringe of long bristles to each joint.

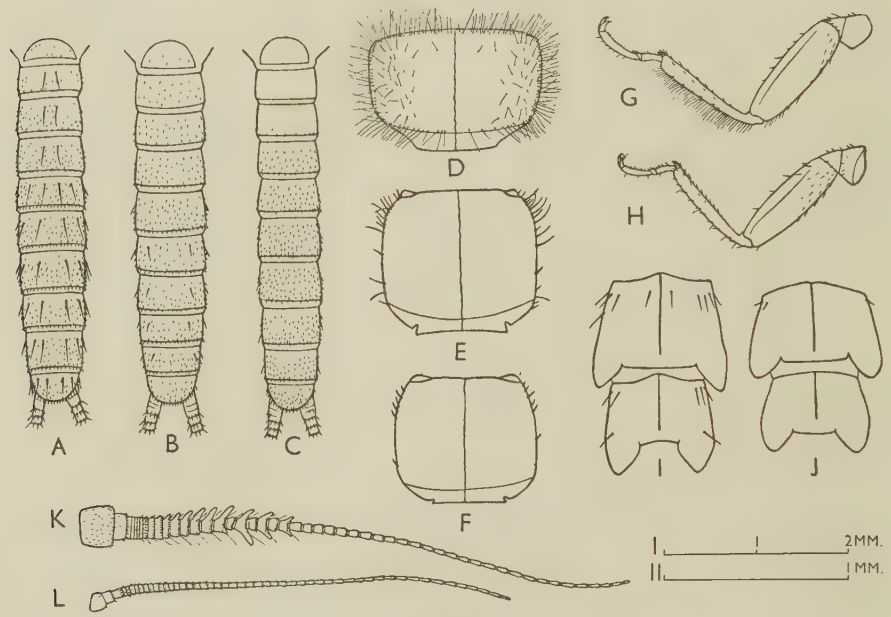

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Fig. 13.—*Leuctra*. A, *L. inermis*, full-grown abdomen in dorsal view (I, s); B, *L. hippopus*, full-grown abdomen in dorsal view (I, s); C, *L. moselyi*, full-grown abdomen in dorsal view (I, s); D, *L. nigra*, pronotum in dorsal view (II, s); E, *L. hippopus*, pronotum in dorsal view (II, s); F, *L. moselyi*, pronotum in dorsal view (II, s); G, *L. fusciventris*, hind leg (I, cl); H, *L. hippopus*, hind leg (I, cl); I, *L. fusciventris*, meso- and metanota of 4¼-mm. nymph (II, cl); J, *L. moselyi*, meso- and metanota of 4¼-mm. nymph (II, cl); K, *L. geniculata*, antenna (I, cl); L, *L. hippopus*, antenna (I, cl).

The young stages are similar, but the meso- and metanotal bristles are more prominent, and the clothing hairs on the terga are absent below 5 mm. Ocelli appear at 4 mm. In the early instars the number of cercal joints is very few, being only four at eclosion.

Nymphs of this species collected in the following vice-counties have been examined: Cumberland (CU), Westmorland + N. Lancs (WL), Wicklow (WI), and Dublin (DU).

Nymphal syntypes, WL, R. Rothay, 22.iv.1940, full-grown nymphs (9 ex.) (*Hynes*).

This species grows during the winter and spring and emerges in the early summer.

Leuctra fusciventris Stephens, 1836 (figs. 12D–I, 13G, and 13I).

= *klapaleki* Kempny, 1898.

Leuctra klapaleki Kemp., Neeracher 1910.

Size of full-grown nymph 6·5–9·0 mm.

General colour grey-brown above with paler wing pads and the head slightly darker, and yellow below; appendages yellow.

Head rounded; antennae slender and straight. A few bristles behind the eyes and one at the base of each antenna. Ocelli black and well defined.

Pronotum quadrate, wider than long, with about 15 bristles on each lateral margin. Meso- and metanota with a few antero-lateral bristles, those on the metanotum being small and inconspicuous.

Legs with scattered bristles and a fringe of long hairs down the posterior margin of the tibia and tarsus.

Abdominal terga, except occasionally the first, covered with fine clothing hairs. The terga of the posterior segments usually have one or two pairs of long lateral bristles about half-way down their length. Cerci with an apical fringe of long bristles to each joint.

The young stages differ from the grown nymphs in the absence of ocelli, which appear at 4 mm., and of the fringe of hairs on the tibiae, which appear at 5 mm. The abdominal and notal bristles are conspicuous below 5 mm., enabling the species to be separated from *L. moselyi*. Below 5 mm. clothing hairs are absent from the anterior abdominal segments.

Nymphs of this species collected in the following vice-counties have been examined: Cumberland (CU), Westmorland + N. Lancs (WL), Caithness (CA), S. Aberdeen (AS), S. Hants (SH), and Perthshire (PC).

Nymphal syntypes, WL, R. Rothay, 16.viii.1940, full-grown nymphs (39 ex.) (*Hynes*).

This species grows during the summer, and adults emerge in the autumn.

Leuctra hippopus Kempny, 1899 (figs. 12 C and J, 13 B, E, H, and L).

Leuctra hippopus Kemp., Klefisch 1915.
Leuctra hippopus Kemp., Kühtreiber 1934.

Size of full-grown nymph 6·0–8·5 mm.

General colour grey-brown above with paler wing pads, and yellow or pale rose-coloured below; appendages yellow or slightly rose-coloured.

Head rounded; antennae slender and straight. A few bristles behind the eyes and one on the base of each antenna. Ocelli black and well defined.

Pronotum quadrate, wider than long, with 15 or more bristles on each lateral margin. Meso- and metanota with a few antero-lateral bristles, those on the metanotum being small and inconspicuous.

Legs with scattered bristles and one or two long hairs on the posterior margin of the tibia.

Abdominal terga, except occasionally the first, covered with fine clothing hairs. The terga of the posterior segments usually have one or two pairs of long lateral bristles about half-way down their length. Cerci with an apical fringe of bristles to each joint.

The young stages differ from the grown nymphs in the absence of ocelli, which appear at 4 mm., and in that the notal bristles are longer and more prominent. Below 5 mm. clothing hairs are absent from the anterior abdominal segments.

Nymphs of this species collected in the following vice-counties have been examined: Cumberland (CU), Westmorland + N. Lancs (WL), Caithness (CA), S. Aberdeen (AS), Wicklow (WI), and Kildare (KD).

Nymphal syntypes, WL, Wray, Boathouse 2 Beck, 19.ii.1940, full-grown nymphs (20 ex.) (*Hynes*).

This species grows during the winter and early spring, and adults emerge in the spring and very early summer.

Leuctra moselyi Morton, 1929 (fig. 13 F and J).

Size of full-grown nymph 6·0–8·5 mm.

General colour grey-brown above with paler wing pads, and yellow or rose-coloured below; appendages yellow or slightly rose-coloured. Across the head in the region of the ocelli there is, in many specimens, an obscure dark mark, enabling the species to be recognised at once.

Head rounded; antennae slender and straight. A few bristles behind the eyes and one at the base of each antenna. Ocelli brown and poorly defined, being often paler in the middle and so appearing as rings.

Pronotum quadrate, wider than long, with 3–11 bristles on each lateral margin. Mesonotum with two or three antero-lateral bristles, metanotum usually without bristles, but very rarely one very small bristle is present on each side.

Legs with scattered bristles and one or two long hairs on the posterior margin of the tibia.

Abdominal terga 4–10 covered with fine clothing hairs, terga 1 and 2 glabrous, and tergum 3 in well-grown nymphs with a few clothing hairs on the posterior margin. The terga of the posterior segments occasionally have one or two pairs of lateral bristles about half-way down their length. Cerci with an apical fringe of bristles to each joint.

The young stages are similar to the grown nymphs, but below 4 mm. have no ocelli. As in the other species, the abdominal clothing hairs are less developed.

Nymphs of this species collected only in Westmorland + N. Lancs (WL) have been examined.

Nymphal syntypes, WL, High Wray Beck, 27.vii.1940, full-grown nymphs (12 ex.) (*Hynes*).

This species grows during the spring and early summer, and adults emerge in late summer and early autumn.

9. Nemouridae Klapálek, 1909.

Nymphs of the species belonging to this family have been known for over a century (Pictet, 1832), and those of many species have since been described. The family has been included in keys by several authors (Klapálek, 1909, Rousseau, 1921, Kühtreiber, 1934), but as explained above (p. 474), the characters given are not satisfactory, and new ones have been proposed.

The family is characterised by the well-developed glossae (figs. 14I, 15I, 16H, and 18H), the subquadrate labrum which is less than twice as wide as long (figs. 14E, 15E, 16D, and 18D), the reduced 10th abdominal sternum (figs. 14 B and C, 15 B and C, 16 B and C, and 18 B and C), the wing pads held obliquely to the body (figs. 14A, 15A, 16A, and 18A), the simple tarsal claws and the proportions of the tarsal joints the 2nd of which is shorter than the 1st (figs. 14 J and K, 15 J and K,16K, and 18J), and the fact that the hind leg when stretched back alongside the abdomen extends far beyond its tip. The mouth-parts, which are uniform throughout the family, are characterised by the well-developed mandibles and the short flattened labial palps (figs. 14 E–I, 15 E–I, 16 D–H, and 18 D–H).

For reasons stated above (p. 471) the four subgenera of the one European genus *Nemoura* Latreille 1802 are treated here as genera, as is the practice of many European workers.

Protonemura Kempny, 1898.

Pictet (1842) first described the nymphs of a species now placed in this genus, and several species have been described since. Kühtreiber (1934) has described six Austrian species and given a table by which they can be separated.

The genus is characterised by the presence of three sausage-shaped prosternal gills on each side, which arise two on the outside and one on the inside of the dorsal cervical sclerite (fig. 14D). According to Kühtreiber the detailed shape of these gills varies with the species, but in both the British species each is an elongate process slightly constricted about one-third of its length from the tip. Gills are absent from the first instar nymphs of *P. praecox*, but at 1·5 mm. they are present, although the outer gill on each side is somewhat shorter than the inner two. In the older nymphs all three gills are the same length. In other characters this genus resembles other members of the family, being stout and dull coloured, and covered with Indian-club-shaped bristles (fig. 2G), which become more pointed towards the tip of the abdomen. There is a well-developed fringe to the pronotum, and the bristles at the tip of each cercal joint are shorter than those in the other genera. The sexes are distinguishable in specimens over 4·5 mm., the hind margin of the 9th abdominal sternum of the male being drawn out backwards to a point and somewhat keeled (fig. 14B), while in the female a small transverse thickening is present on the 8th sternum (fig. 14C).

Two species of the genus are recorded as British (Kimmins, 1940).

Keys to species.

Specimens over 4 mm.

1 (2). General colour dark green-grey, abdominal segments 1–4 divided into tergum and sternum (fig. 14M) (segments 5–8 usually show partial division, but this is never complete). Tarsi darkened on the upper-side (fig. 14K), distal cercal joints darkened at the tips and bases so that the cercus is ringed (fig. 14A), antennae darkened distally. Abdominal terga with a simple fringe of bristles on the posterior margin, one or two of which may be longer than the others, but never more than twice as long. Male sub-anal plates slightly emarginate at the tip (fig. 14C) . . . . . *P. meyeri* (Pict.) (p. 508).

2 (1). General colour rufous brown. Abdominal segments 1–5 divided into tergum and sternum (fig. 14L) (segments 7 and 8 never show partial division). Tarsi (fig. 14J), cerci, and antennae uniformly yellow. Abdominal terga 2 or 3 to 7, 8, or 9 bearing a long dorso-lateral bristle on each side of the posterior margin, which is two or three times as long as the other bristles in the posterior fringe. Sub-anal plates simple and rounded at the tip in both sexes.
P. praecox (Mort.) (p. 508).

Specimens 1–4 mm.

1 (2). On all the abdominal terga the bristles of the posterior fringe of varying length, no single bristle being much longer than the others (fig. 14O). Division of the abdominal segments and coloration as in the above key. . . . . *P. meyeri* (Pict.) (p. 508).

2 (1). Abdominal segments 2–3 bearing, on each side of the posterior margin, one, or rarely two, long dorso-lateral bristles, each of which is two or three times as long as the other bristles in the posterior fringe (fig. 14N). Division of the abdominal segments and coloration as in the above key . . . . . *P. praecox* (Mort.) (p. 508).

Protonemura meyeri (Pictet, 1842) (figs. 14 A–D, K, M, and O).

Size of full-grown nymph 8–10 mm., the females usually being slightly larger than the males.

General colour dark green-grey, with a few darker marks on the nota; appendages grey to yellow.

Head wider than long, and rounded. Dorsal callosities, which are darker coloured than the rest of the head, more or less crescentic. Antennae about as long as the thorax and darkened towards the tip. Mouth-parts brown.

Pronotum quadrate, with a well-developed fringe of bristles, and a few curved darker lines laterally. Meso- and metanota with bristles anteriorly. Wing pads often lighter coloured than the nota, and in well-grown specimens the darkening of the wing membrane round the veins, which is characteristic of the adults, becomes visible.

Legs grey and stout, covered with bristles except on the femoral and tibial lines. On the anterior face of the fore femur is a conspicuous white triangular patch. Tarsi conspicuously darkened along the dorsal side.

Abdomen cylindrical. Segments 1–4 only divided into tergum and sternum; segments 5–8 may be partially divided, especially in small specimens. Each tergum is covered with clothing hairs, and has a fringe of bristles posteriorly, which extends round on to the sternum on each side in the posterior segments. In some specimens one dorso-lateral bristle on each side in the posterior fringe of each segment may be enlarged, but it is never two or three times as large as the other bristles in the fringe. The sexes differ as described above (p. 507); the sub-anal plates are longer than wide, rounded at the tip in the female, and emarginate at the tip in the male. Cerci as long as the abdomen; each joint darkened at the base and at the tip, making the cercus appear ringed.

Specimens below 4 mm. are similar in form and general structure to the grown nymphs, but the bristles are longer in proportion to the rest of the body, and it is not always possible to make out the division of the abdominal segments into tergum and sternum. Similarly, the colour is much paler, and in specimens below 2 mm. the darkening of the cerci and tarsal joints may be difficult to see. On the abdominal terga only scattered clothing hairs are present, but the posterior fringe of bristles is well developed, and composed of bristles of varying length (fig. 14O). Ocelli appear at 2 mm.

Nymphs of this species collected in the following vice-counties have been examined: Cumberland (CU), Westmorland + N. Lancs (WL), Wicklow (WI), and Kildare (KD).

Nymphal syntypes, WL, R. Rothay, 22.iv.1940, full-grown nymphs (3 ♂, 3 ♀) (*Hynes*).

The shape of the gills (p. 507) and the sub-anal plates of the male, and the absence of long dorso-lateral abdominal bristles would enable this species to be separated from the six Austrian species described by Kühtreiber (1934).

Protonemura praecox (Morton, 1894) (figs. 14 E–J, L, and N).

Protonemura praecox Mort., Mertens 1921 and 1923.
Protonemura praecox Mort., Kühtreiber 1934.

The nymphs of this species are similar in size and general form to those of *P. meyeri*, and differ only from that species as described above in the following particulars.

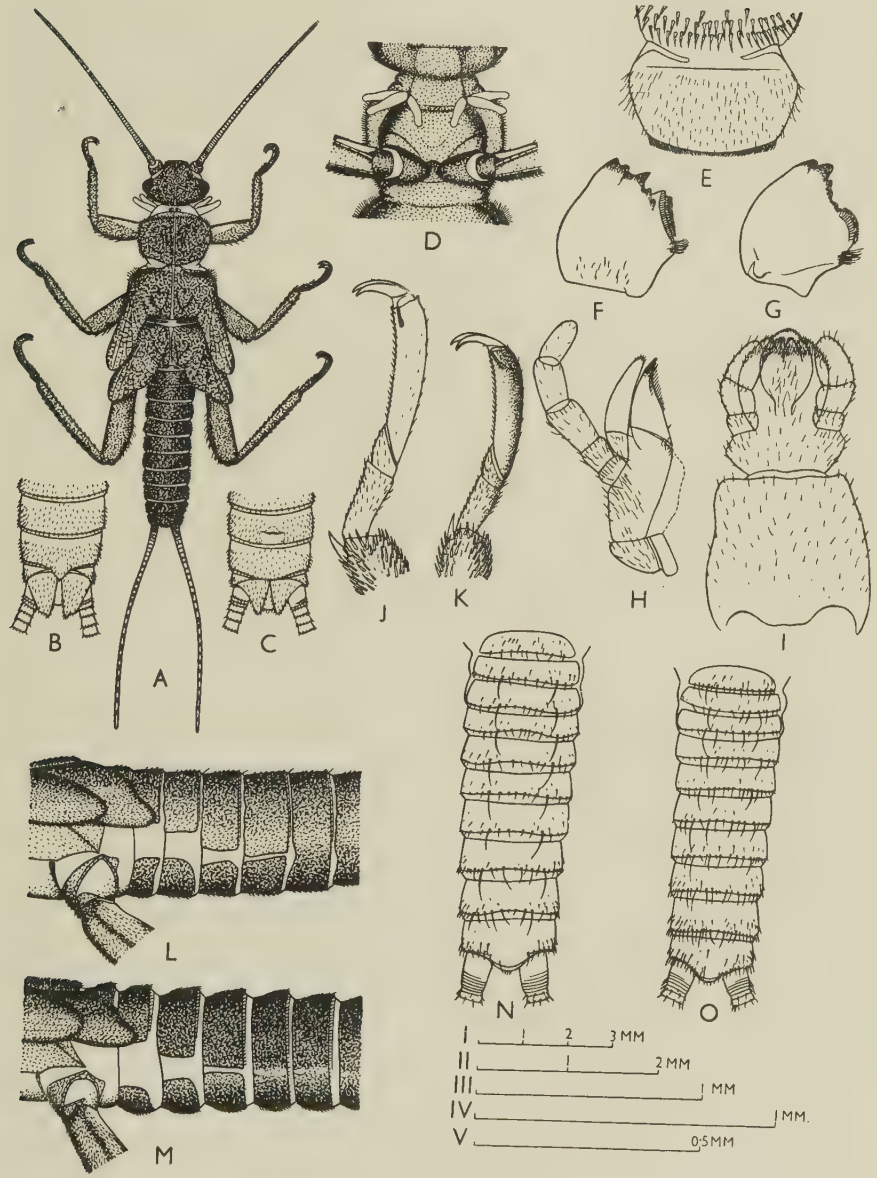

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FIG. 14.—*Protonemura*. A–D, *P. meyeri*: A, Full-grown nymph in dorsal view (I, s); B, Tip of full-grown male abdomen in ventral view (II, s); C, Tip of full-grown female abdomen in ventral view (II, s); D, Prothorax in ventral view (II, s); E–I, *P. praecox* mouth-parts (V, cl): E, Labrum in dorsal view; F, Left mandible in dorsal view; G, Right mandible in ventral view; H, Right maxilla in ventral view; I, Labium, with hypopharynx attached, in ventral view; J, *P. praecox*, hind tarsus (III, cl); K, *P. meyeri*, hind tarsus (III, cl); L, *P. praecox*, base of abdomen in lateral view (II, s); M, *P. meyeri*, base of abdomen in lateral view (II, s); N, *P. praecox*, abdomen of $2\frac{3}{4}$-mm. nymph in dorsal view (IV, cl); O, *P. meyeri*, abdomen of $2\frac{3}{4}$-mm. nymph in dorsal view (IV, cl).

General colour dark rufous brown with paler wing pads, which are without any darkening along the veins; appendages yellowish. Antennae, tarsi and cerci uniformly yellow. Abdominal segments 1–5 divided into tergum and sternum; segments posterior to this, with the exception of segment 6, which may be partly divided in small specimens, are fused into complete rings. Sub-anal plates in both sexes rounded at the tip, and wider than long when pressed out flat. All the abdominal segments have a sparse covering of clothing hairs and a posterior fringe of bristles; on segments 2 or 3 to 7, 8, or 9 one dorso-lateral bristle on each side of this fringe is greatly enlarged, and is two or three times as long as the other bristles in the fringe. These, the "Abdominalpaardornen" of Kühtreiber, are best seen in lateral view.

In specimens below 4 mm., as in *P. meyeri*, the division of the abdominal segments into tergum and sternum is not easily seen, and the species is most readily recognisable by the abdominal bristles (fig. 14N), which resemble those of the grown nymph. Occasionally, however, there are two long dorso-lateral bristles on one or other side of one or two of the segments, and in all specimens several long bristles are present on the posterior segments.

Nymphs of this species collected only in Westmorland + N. Lancs (WL) have been examined.

Nymphal syntypes, WL, Wray, Nor Moss Beck, 1.iii.1939, full-grown nymphs (2 ♂, 2 ♀) (*Hynes*).

British specimens agree closely with the descriptions of this species in Europe by Mertens and Kühtreiber.

Amphinemura Ris, 1902.

The supposed nymphs of *A. cinerea* were described more than a century ago (Pictet, 1832, and 1842), but the descriptions are obviously those of nymphs of a species of *Protonemura*. More recently the true nymphs of *A. cinerea* have been briefly described (Kempny, 1898), and (Klapálek, 1909) and Koponen (1917) has given a careful description of the nymph of *A. standfussi*.

It is impossible, however, with the aid of these descriptions to make a specific identification.

The genus is characterised by the presence of two stalked bunches of 5–8 filamentous gills on each side of the prosternum. One bunch arises on the outer side of the dorsal cervical sclerite, and one just posterior to this sclerite (fig. 15D). In young specimens the number of filaments in each of these bunches is fewer, and in 1-mm. specimens there are 2 filaments in the outer bunch and 1 in the inner. Nymphs at this size are, however, still distinguishable from *Protonemura*, because the gills are filamentous and not sausage-shaped. The number of filaments in each gill bunch increases rapidly; at 1·5 mm. there are 4 in the outer and 3 in the inner bunch, and at 4 mm., at which size the wing pads have not yet begun to develop, the full number of filaments is present. There is in all stages a well-developed fringe of bristles to the pronotum. In other characters the genus resembles other members of the family, the chief difference being the slightly fusiform abdomen and the presence of long fine bristles on the posterior margin of each of the abdominal segments. The genus is easily recognisable in the field because it is always covered with flocculent detritus, which sticks to the bristles all over the body and gives the nymph a woolly appearance. Abdominal segments 1–6 are divided into tergum and sternum in the two British species. The sexes are distinguishable in both species, the hind margin of the 9th abdominal sternum being drawn out backwards and somewhat keeled in the male (fig. 15B); in *A. cinerea* the female

shows a small transverse thickening on the cuticle on the 8th sternum (fig. 15C), but this is not present in *A. standfussi*.

Two species of the genus are recorded as British (Kimmins, 1940). It has not been found possible to make a key that will separate all nymphs of these two species, but the following key is probably applicable to most, especially if several specimens from the same locality are examined together.

Key to species.

Specimens over 1 mm.

1 (2). General colour usually chocolate-brown, paler in the smaller specimens. Bristles on all the femora sharply differentiated into large and small bristles, the large bristles being arranged in a group about $\frac{2}{3}$ down the length of the sclerite (fig. 15J) (this is best seen in the hind leg) *A. cinerea* (Oliv.) (p. 511).

2 (1). General colour orange-yellow, yellow in the smaller specimens. Bristles on all the femora not sharply differentiated into two types, and usually evenly distributed, being only slightly thicker about halfway down the sclerite (fig. 15K) (best seen in the hing leg). *A. standfussi* Ris (p. 512).

Amphinemura cinerea (Olivier, 1811) (figs. 15 A–J).

? *Nemoura cinerea* Oliv., Pictet 1842.
Nemoura cinerea Oliv., Kempny 1898.
Amphinemura cinerea Oliv., Klapálek 1909.

Size of full-grown nymph 4–6 mm.

General colour dark chocolate-brown, the wing pads, the edges of the pronotum, the appendages and the underside being lighter.

Head rounded, slightly narrower than the pronotum in the full-grown nymph. Dorsal callosities more or less crescentic.

Pronotum quadrate, with a well-developed fringe of bristles, usually paler on the extreme lateral margins. Meso- and metanota with bristles anteriorly. Gills silver white.

Legs stout and covered with small bristles. On all legs there is a group of large stout bristles on the dorsal and posterior side of the femur, about $\frac{2}{3}$ down its length. Tibiae with a fringe of hairs down the posterior margin.

Abdomen, like the rest of the body, covered with clothing hairs. On the posterior margin of each tergum are a number of long fine outstanding bristles, which are usually covered with flocculent detritus. Sexes distinguishable as described above (p. 510) in specimens over 4·5 mm. Cerci longer than the abdomen and darkened at the base; each joint wider at the tip than at the base, and with an apical whorl of long bristles.

The young stages resemble the well-grown nymphs, but are paler coloured; in specimens below 4 mm. the ocelli are absent, and the number of gill filaments is reduced (p. 510).

Nymphs of this species collected in the following vice-counties have been examined : Cumberland (CU), Westmorland + N. Lancs (WL), S. Hants (SH), Caithness (CA), S. Aberdeen (AS), Wicklow (WI), and Kildare (KD).

Nymphal syntypes, WL, R. Rothay, 23.v.1940, full-grown nymphs (3 ♂, 8 ♀) (*Hynes*).

Pictet's description of the nymph does not agree with British material in that he says that three pairs of prosternal gills are present. This is a character typical of nymphs of *Protonemura*, so it seems that he must have misidentified his nymphs. Klapálek's description agrees with British material, except that he describes the posterior margin of the pronotum as " stumpfwinklig ausge-

schnitten," whereas in British material it is straight. This statement led Koponen (1917) to suppose that the nymph of *A. standfussi* as described by him could be separated from that of *A. cinerea* on the shape of the pronotum. In actual fact his description, although it appears to be thorough, would apply equally well to either species in Britain.

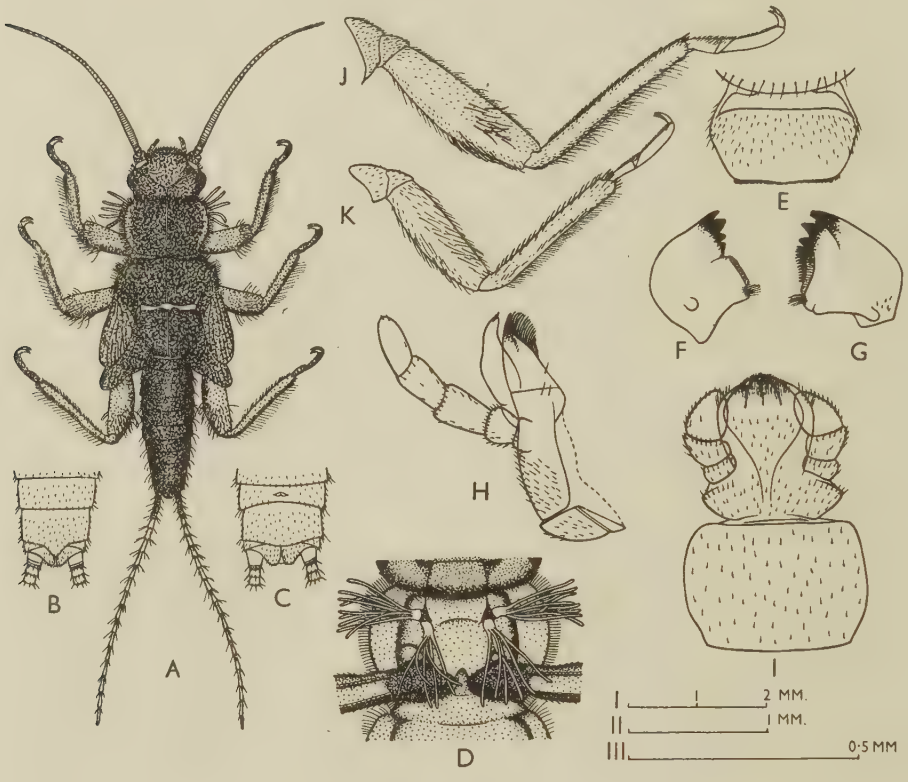

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Fig. 15.—*Amphinemura.* A–I, *A. cinerea*: A, Full-grown nymph (I, s); B, Tip of full-grown male abdomen in ventral view (II, s); C, Tip of full-grown female abdomen in ventral view (II, s); D, Prothorax in ventral view (II, s); E, Labrum in dorsal view (III, cl); F, Right mandible in ventral view (III, cl); G, Left mandible in ventral view (III, cl); I, Labium, with hypopharynx attached, in ventral view (III, cl); J, *A. cinerea*, hind leg (II, cl); K, *A. standfussi*, hind leg (II, cl).

Amphinemura standfussi Ris, 1902 (fig. 15K).

Amphinemura standfussi Ris, Koponen 1917.

The nymph of this species is similar to that of *A. cinerea* as described above, but differs in the following particulars.

Size of full-grown nymph 4·5–5·0 mm. General colour orange-yellow; gills yellowish. Femora of all legs with scattered bristles of varying size, not sharply differentiated into large and small bristles; in most specimens there is no definite grouping of the bristles on any part of the sclerite, but they tend to be more numerous towards the middle. The bristles on all parts of the body are smaller and finer than those of *A. cinerea*, and the long abdominal

bristles are less developed. The sexes are distinguishable as described above (p. 510) at 4 mm.

Nymphs of this species from only one locality on the border of Dorset (DT) and S. Hants (SH) have been examined; collections were made in this locality in May, December, and April, and some of the specimens taken in April were reared to maturity in the laboratory.

Nymphal syntypes, DT/SH, Daggons Brook, 18 or 19.iv.1940, nymphs (3 ♂, 1 ♀) (*J. W. Jones*).

This material agrees well with the description of this species by Koponen, but, as is pointed out above, his description would not enable a specific identification to be made.

Nemoura Latreille, 1802 s.str. (Kempny 1898).

Nymphs belonging to this species in its restricted sense (Kempny, 1898) have been known for over a century (Pictet, 1832), and several species have been briefly described since. Klapálek (1909) has separated *N. marginata* Pict. and *N. variegata* in a key based on the pronotal fringe and the relative lengths of the cercal bristles, and Kühtreiber (1934) has used these and other characters, such as the bristles on the legs and abdomen, to separate six Austrian species. Characters involving the relative lengths of the cercus and its bristles are, however, unsatisfactory, because the number of joints and their relative proportions vary with age, and, as Kühtreiber himself has pointed out, in regenerating cerci, which are frequently found, the proportions are totally different from the normal condition.

The genus is characterised by the absence of prosternal gills, and the fact that in the hind tarsus joint 1 is only about half as long as joint 3 (fig. 16K), and is even smaller in proportion in nymphs under 4 or 5 mm. The general proportions of the nymphs vary with the species, *N. erratica* being stout (fig. 16A), while *N. avicularis* is slender with long antennae and cerci and resembles *Nemurella* in general shape (fig. 18A). The sexes are distinguishable above 5 mm. in all species except *N. cambrica*, in which they are distinct at 4·5 mm. In the male of all species the hind margin of the 9th abdominal sternum is drawn out backwards into a point and is slightly keeled (fig. 16B), and in the female the hind margin of the 7th abdominal sternum is drawn out backwards into a wide subgenital plate (fig. 16C), the shape of which varies with the species. In the four British species of which nymphs have been obtained abdominal segments 1–6 are divided into tergum and sternum.

There are five species on the British list, and one, *N. marginata* Pict., which has been recorded here in error (Kimmins, 1940, and Hynes, 1940). Nymphs of four of the five species have been obtained; the fifth species is rare, and is confined in Britain to Suffolk. Keys to the nymphs of the four common species are given.

Keys to species.

Specimens over 5 mm.

1(4). Each femur with long curved bristles on its distal half, and shorter bristles proximally (fig. 16I). (Stout-bodied species living in small stony streams.)

2(3). Dorsal callosities, which are dark coloured at this size, crescent-shaped (fig. 17D) . . . . . *N. cambrica* Steph. (p. 516).

3(2). Dorsal callosities, which are dark coloured at this size, more or less triangular (fig. 17C) . . . . . *N. erratica* Claas. (p. 515).

4(1). Each femur usually covered with fine bristles of about equal length (fig. 16J). (More slender species with long legs and antennae.)

5(6). 2nd antennal joint much darker coloured than the 1st (fig. 17B) (the basal joints of the flagellum may be darkened also). Ocelli indistinct or invisible. Cercal bristles long and fine, not much darker coloured than the cercus. (Species with very long legs, antennae, and cerci; usually dull olive-grey coloured; living on the stony shores of lakes or in the vegetation in sluggish rivers and streams.) *N. avicularis* Mort. (p. 518).

6(5). 2nd antennal joint not darker coloured than the 1st (fig. 17A). Ocelli distinct. Cercal bristles stout and darker coloured than the cercus. (Variable species; usually pale brown and shiny; living in the submerged parts of emergent vegetation in still or slowly running water.) *N. variegata* (Oliv.) (p. 516).

Specimens 3–5 mm.

1(2). 2nd antennal joint much darker coloured than the 1st (fig. 17B). Cercal bristles long and fine, not much darker coloured than the cercus. (Species with very long legs, antennae, and cerci; usually dull olive-grey coloured; ocelli invisible; living on the stony shores of lakes or in the vegetation in sluggish rivers and streams.) *N. avicularis* Mort. (p. 518).

2(1). 2nd antennal joint not darker coloured than the 1st (figs. 17A, C, and D). Cercal bristles stout, darker coloured than the cercus.

3(4). Ocelli clearly visible as black spots on a pale brown background; head uniformly brown except for a darker area round the dorsal callosities (fig. 17A). (Species living in the submerged parts of emergent vegetation in still or slowly running water.) . . *N. variegata* (Oliv.) (p. 516).

4(3). Ocelli absent, or if present indistinct and not darker coloured than the background; head with at least traces of a dark-coloured transverse band between the eyes (this band may be partly obscured in larger specimens by the general darkening of the head). (Stout-bodied species living in small stony streams.)

5(6). Dorsal callosities, which are dark coloured in larger and pale in smaller specimens, crescent-shaped (fig. 17D). . . *N. cambrica* Steph. (p. 516).

6(5). Dorsal callosities, which are usually pale coloured at this size, more or less triangular (fig. 17C) . . . . . *N. erratica* Claas. (p. 515).

Specimens 1–3 mm.

1(2). 2nd antennal joint much darker coloured than the 1st (fig. 17B). Cercal bristles long and fine. (Species with very long legs, antennae, and cerci; ocelli absent; with a distinct dark-coloured band across the head between the eyes; living on the stony shores of lakes or in the vegetation in sluggish rivers and streams.) *N. avicularis* Mort. (p. 518).

2(1). 2nd antennal joint not darker coloured than the 1st (figs. 17A, C, and D). Cercal bristles stout.

3(4). Head without a distinct dark-coloured transverse band between the eyes; ocelli present (fig. 17A). (Species living in the submerged parts of emergent vegetation in still or slowly running water.) *N. variegata* (Oliv.) (p. 516).

4(3). Head with a distinct dark-coloured transverse band between the eyes; ocelli absent (fig. 17 C and D). (Stout-bodied species living in small stony streams.)

5(6). Dorsal callosities, which are pale and stand out clearly in the dark band, crescent-shaped (fig. 17D) . . . . . *N. cambrica* Steph. (p. 516).

6(5). Dorsal callosities, which are pale and stand out clearly in the dark band, more or less triangular (fig. 17C) . . . . *N. erratica* Claas. (p. 515).

Nemoura erratica Claassen, 1936 (figs. 16 A–C and K, and 17C).

= *risi* Despax, 1929 and 1934.

Size of full-grown nymph 6·5–9·0 mm.

General colour dark rufous brown above, paler below; appendages yellow to brown.

Head wide and rounded, dorsal callosities large and more or less triangular. Ocelli indistinct because they are the same colour as the surrounding cuticle.

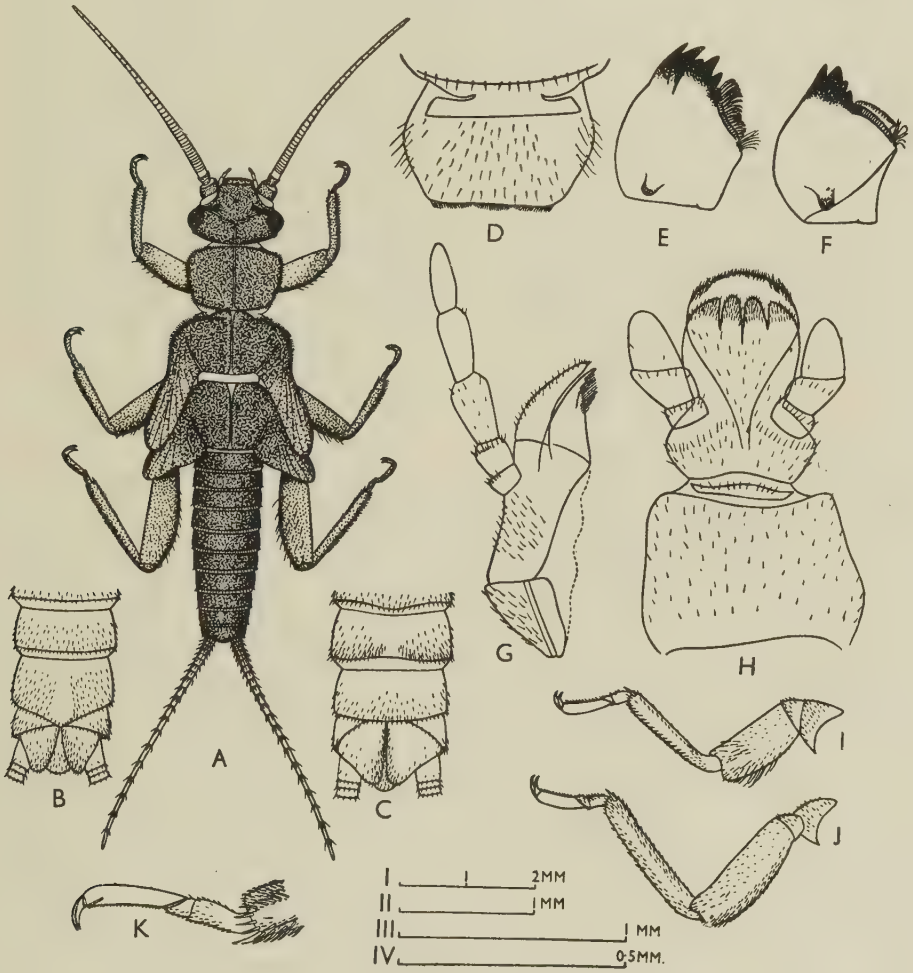

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Fig. 16.—*Nemoura.* A–C, *N. erratica*: A, Full-grown nymph (I, s); B, Tip of full-grown male abdomen in ventral view (II, s); C, Tip of full-grown female abdomen in ventral view (II, s); D–H, *N. avicularis*, mouth-parts (IV, cl): D, Labrum in dorsal view; E, Right mandible in ventral view; F, Left mandible in dorsal view; G, Right maxilla in ventral view; H, Labium, with hypopharynx attached, in ventral view; I, *N. cambrica*, fore leg (II, cl); J, *N. variegata*, fore leg (II, cl); K, *N. erratica*, hind tarsus (III, cl).

Pronotum quadrate, with a well-developed fringe of small bristles. Meso- and metanota with small bristles anteriorly; wing pads lighter coloured than the nota.

Legs stout and covered with bristles; femur of each leg with a group of long stout curved bristles on the upper and posterior side of its distal half (as fig. 16I). Fore femur with a pale-coloured triangular patch anteriorly.

Abdomen cylindrical, covered, as is the rest of the body, with clothing hairs. On the posterior margin of each tergum is a fringe of bristles, one of which on each side is often enlarged (cf. *P. praecox*). Cerci as long as abdomen, darkened at the base; each joint with an apical whorl of stout dark-coloured bristles.

Specimens below about 4·5 mm. have a dark brown band across the head between the eyes on which the dorsal callosities, which are larger in proportion to the head than in the full-grown nymph, stand out as yellow spots. As the nymph grows the colour darkens from pale yellow-brown to dark red-brown, and the dark band across the head becomes obscured, disappearing at about 4·5 mm. At the same time, the colour of the dorsal callosities darkens rapidly, and above 5 mm. they become darker than the rest of the head. Ocelli can first be seen at 4·5 mm.

Nymphs of this species collected in the following vice-counties have been examined: Cumberland (CU), Westmorland + N. Lancs (WL), and Surrey (SR).

Nymphal syntypes, WL, Wray, Boathouse 2 Beck, 23.iii.1939, full-grown nymphs (2 ♂, 3 ♀) (*Hynes*).

Nemoura cambrica Stephens, 1836 (figs. 16I and 17D).

Nemura cambrica Mort., Kühtreiber 1934.

The nymphs of this species are very similar to those of *N. erratica*, but differ from that species as described above in the following particulars.

Size of full-grown nymph 5–6 mm. Dorsal callosities narrow and crescentic. In the ripe female nymph the lobe on the posterior margin of the 7th abdominal sternum is wider than that of *N. erratica* (fig. 16C).

Nymphs below 3·5 mm. show a distinct dark-coloured band across the head between the eyes, on which, as in *N. erratica*, the dorsal callosities stand out as pale spots. This band is, however, darker coloured than that of *N. erratica*, particularly posteriorly, and its posterior margin is usually still visible in the full-grown nymph. The dorsal callosities darken as in *N. erratica*, and above 4 mm. are darker coloured than the rest of the head.

Nymphs of this species collected in the following vice-counties have been examined: Cumberland (CU), Westmorland + N. Lancs (WL).

Nymphal syntypes, WL, Wray, Boathouse 2 Beck, 16.iv.1940, full-grown nymphs (4 ♂, 4 ♀) (*Hynes*).

British material agrees closely with the description by Kühtreiber of Austrian nymphs of this species.

Nemoura variegata (Olivier, 1811) (figs. 16J and 17A).

Nemura variegata Oliv., Pictet 1832 and 1842.
Nemura variegata Oliv., Klapálek 1909
Nemura variegata Pict., Kühtreiber 1934.

Size of full-grown nymph 5–9 mm.

General colour light brown above, paler below; appendages yellow to brown; cuticle usually shiny.

Head rounded; dorsal callosities crescentic (fig. 17A). Ocelli dark brown and distinct. Antennae long; joints 1 and 2 similarly coloured but often darker than the rest of the antenna.

Pronotum quadrate, without a fringe of bristles, or if a fringe is present it is poorly developed; usually with a few dark marks on each side. Meso- and metanota with small bristles anteriorly; wing pads paler than the nota.

Legs less stout than in *N. erratica* and *N. cambrica* and covered with small bristles, which are evenly distributed over the femora.

Abdomen cylindrical, covered with small clothing hairs. On the posterior margin of each tergum is a fringe of bristles, one of which on each side is often somewhat enlarged (cf. *P. praecox*). Cerci 1·5 times as long as the abdomen; each joint with an apical whorl of stout dark-coloured bristles.

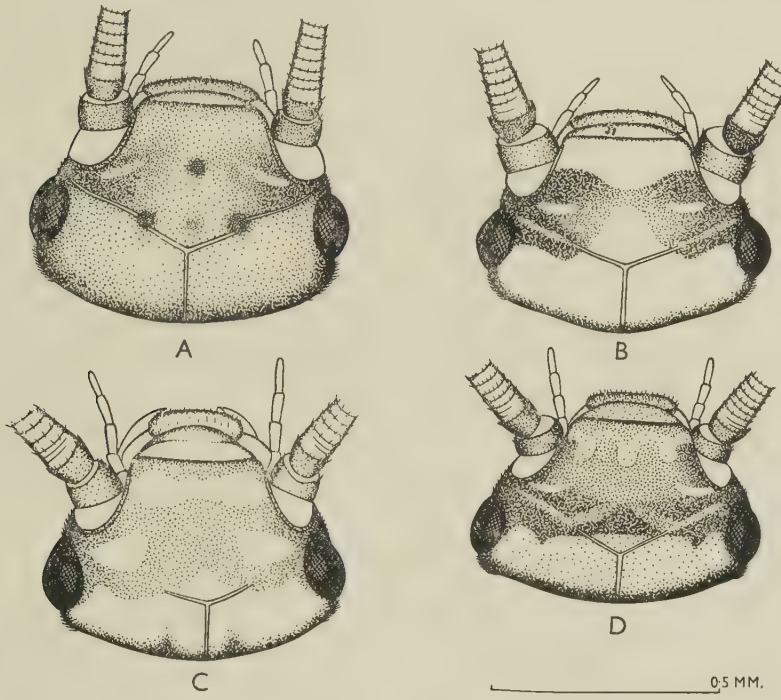

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Fig. 17.—*Nemoura*. Heads of 3-mm. nymphs (cl); A, *N. variegata*; B, *N. avicularis*; C, *N. erratica*; D, *N. cambrica*.

Specimens below 5 mm. are similar in general form to the well-grown nymphs, but the bristles on the femora are often more prominent. Unlike the other species, there is no definite dark-coloured band across the head, which is light brown and only darkened in the region of the dorsal callosities. Ocelli are clearly visible at 1·5 mm. and can be made out down to 1 mm. In the early stages the dorsal callosities are pale, but they darken as in *N. erratica*.

Nymphs of this species collected in the following vice-counties have been examined: Cumberland (CU), Westmorland + N. Lancs (WL), Surrey (SR), S. Hants (SH), Wicklow (WI), and N. Galway (NG).

Nymphal syntypes, WL, Blelham Fish Pond, 19.iv.1939, nymphs (4 ♂, 4 ♀) (*Hynes*).

British material agrees with the descriptions of Klapálek and Kühtreiber. Pictet's description is too brief to give anything but generic characters.

Nemoura avicularis Morton, 1894 (figs. 16 D–H and 17B).

Nemura avicularis Mort., Petersen 1910.

Size of full-grown nymph 7–8 mm.

General colour dull olive-grey, paler below; appendage grey; cuticle not shiny.

Head rounded, dorsal callosities narrow and crescentic. Ocelli obscure, being the same colour as the head, and usually difficult to see. Antennae long; 2nd joint, and sometimes one or two of the following joints, much darker coloured than the rest of the antenna.

Pronotum quadrate, usually without a fringe of bristles. Meso- and metanota with small bristles anteriorly; wing pads paler coloured than the nota.

Legs long and slender compared with those of the other species, and covered with small fine bristles, which are uniformly distributed over the femora (as fig. 16J).

Abdomen cylindrical, covered with fine clothing hairs. On the posterior margin of each tergum is a fringe of bristles, one of which on each side is usually enlarged (cf. *Pr. praecox*). Cerci twice as long as the abdomen; each segment with an apical whorl of long pale-coloured silky bristles.

Specimens below 5 mm. are paler coloured than the full-grown nymphs, and have antennae and cerci which are about twice as long as the body. Below 4 mm. ocelli are absent, and there is a characteristically shaped dark-coloured band across the head between the eyes (fig. 17B). Even at 1 mm., at which size the general colour of the nymph is almost white, the 2nd joint of the antenna is clearly darkened.

Nymphs of this species collected only in Westmorland + N. Lancs (WL) have been examined.

Nymphal syntypes, WL, Windermere, 9.iv.1940, nymphs (3 ♂, 3 ♀) (*Hynes*).

Nemoura dubitans Morton, 1894

The nymph of this species, which is recorded in Britain from only two localities in Suffolk (Kimmins, 1940), is unknown. One of the localities, a field dyke at Fritton, was visited in March 1940 in the company of Mr. C. Morley, who found several adults of the species on *Salix* bushes there in 1936, but no stoneflies or their nymphs were found. The dyke was stagnant and full of rotting leaves and *Lemna trisulca*, and appeared to be a most unusual habitat for stoneflies.

Nemurella Kempny, 1898.

The supposed nymphs of *Nemurella* were described by Pictet (1842), but as he mentions gills of the type found in *Protonemura*, it seems that his specimens were misidentified. Later descriptions of the only European species of the genus agrees closely with British material. The genus has been included in keys by Lestage (Rousseau, 1931) and Klapálek (1909), who used the length of the sub-anal plates of the male and the proportions of the joints of the hind tarsus as their characters. Unfortunately neither of these characters is applicable to the young nymphs, because the sexual distinctions do not develop until 5 mm., and the proportions of the tarsal joints in the hind leg of small specimens are the same as those found in *Nemoura*. It is, however, possible in Britain to use a femoral character mentioned by Kühtreiber (1934) to separate the young stages.

The genus is characterised by the absence of prosternal gills, and the fact

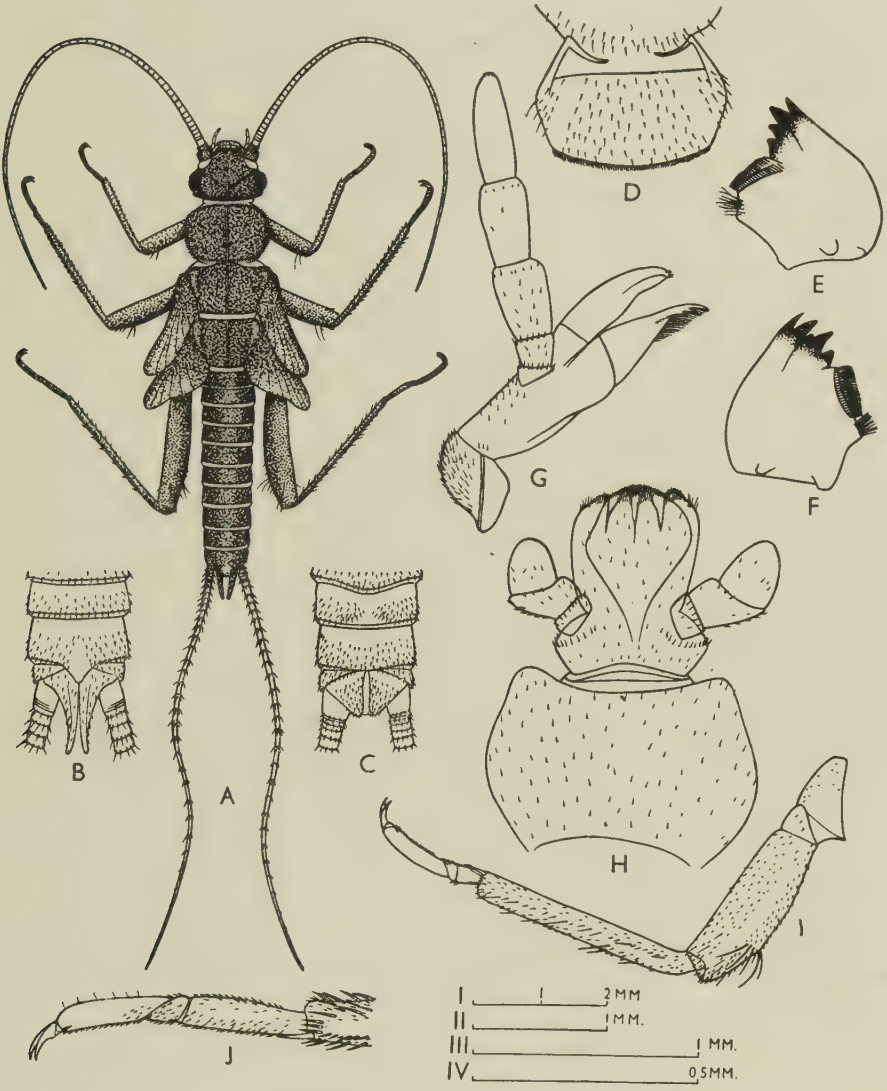

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Fig. 18.—*Nemurella inconspicua*. A, Full-grown male nymph (I, s); B, Tip of full-grown male abdomen in ventral view (II, s); C, Tip of full-grown female abdomen in ventral view (II, s); D, Labrum in dorsal view (IV, cl); E, Left mandible in dorsal view (IV, cl); F, Right mandible in dorsal view (IV, cl); G, Right maxilla in ventral view (IV, cl); H, Labium, with hypopharynx attached (IV, cl); I, Middle leg of 5-mm. nymph (III, cl); J, Hind tarsus of full-grown nymph (III, cl).

that in the hind tarsus of specimens over 5 mm. the first and third joints are subequal, the second being short (fig. 18J); below 5 mm. the first joint is shorter than the third, and at 1·5 mm. it is less than half as long. In all specimens, on at least some of the legs, there is a transverse row of long stout

bristles across the dorsal side of the femur about $\frac{3}{4}$ down its length. Abdominal segments 1–6 are divided into tergum and sternum.

The one species of this genus is common in Britain (Kimmins, 1940).

Nemurella inconspicua (Pictet, 1836) (fig. 18).

= *picteti* Klapálek 1909.

? *Nemura inconspicua* Pict., Pictet 1842.
Nemura (*Nemurella*) *picteti* Klapálek 1909.
Nemurella picteti Klap., Kühtreiber 1934.

Size of full-grown nymph 7–9 mm.

General colour grey-brown to dark grey, with grey to dark grey appendages.

Head rounded; antennae long; dorsal callosities narrow and crescentic. Ocelli distinct, but not much darker coloured than the rest of the head.

Pronotum quadrate, with a well-developed fringe of bristles. Meso- and metanota with bristles anteriorly. Wing pads usually paler coloured than the nota.

Legs long and slender, with a few scattered bristles, and several longer bristles on the tibia; across the dorsal side of the tibia, about $\frac{3}{4}$ down its length, is a row of long stout curved bristles. Hind tarsi with joints 1 and 3 subequal.

Abdomen cylindrical, covered with clothing hairs; each tergum with a posterior fringe of small bristles, one of which on each side of segments 1–9 is enlarged. In the male the hind margin of the 9th sternum is drawn out backwards into a point, the sternum is somewhat keeled, and the sub-anal plates are greatly elongated; in the female the 9th sternum and the sub-anal plates are simple, but the hind margin of the 7th sternum is drawn out backwards. Cerci about $\frac{3}{4}$ as long as the body and darkened at the base; each joint with an apical whorl of stout curved bristles.

Specimens below 5 mm. are pale brown and differ slightly from the full-grown nymphs. Ocelli are present at 1 mm., but at this size the first tarsal joint of the hind leg is less than twice as long as the third. The proportionate length of the first tarsal joint increases with age, and at 5 mm. the first and third joints are subequal. At 4 mm. the sub-anal plates of the male become elongated, and those of the female become more pointed than those of smaller specimens. As in *N. variegata*, there is no distinct dark-coloured band across the head in small specimens, but there is a darker patch round each dorsal callosity and often a dark patch between the ocelli.

Nymphs of this species collected in the following vice-counties have been examined: Cumberland (CU), and Westmorland + N. Lancs (WL).

Nymphal syntypes, WL, Wray, Sign Post Trickle, 20.ix.1939, full-grown nymphs (3 ♂, 3 ♀) (*Hynes*).

IV. Ecology of the Nymphs.

1. Classification of habitats.

It is desirable, in the classification of aquatic habitats, to adopt some uniform method of separating localities which is applicable to both regional and local hydrobiology. Moon (1939) suggests that in the classification of streams and lake shores, erosion and the deposition of silt are the factors on which classification should be based, but while this arrangement seems to be satisfactory for a major classification, it does not give any obvious method by which detailed classification can be made. Most stonefly nymphs inhabit waters with a stony substratum, which in Moon's classification would rank as unsilted localities. But many such localities are to a certain extent silted, the silt being held up in packets of decaying leaves and grass; in fact, the food of many animals in such

localities is silt and decaying leaves, and not the diatoms and other algae encrusting the stones, as is stated by Moon. Accordingly, while agreeing with Moon, that the substratum is the most important ecological factor in such localities, it has not been found possible to base a classification of the habitats of stonefly nymphs on his scheme.

This study of the ecology of the nymphs of stoneflies has been carried out almost entirely in the Lake District as defined by Macan (1940), only occasional collections being made in other parts of the country; but the results of such collections have always agreed closely with those of collections made in similar localities within the Lake District. It seems probable, therefore, that the following classification of habitats will apply, at least in outline, to stonefly habitats throughout Britain. It is obviously impossible at the present stage of hydrobiological research to produce a detailed classification which is infallible, because the actual factors controlling the distribution of many aquatic animals are quite unknown, and this applies especially to the stream fauna to which most stoneflies belong. Habault (1927) and Hora (1930) have both written on this subject, but neither has come to any definite conclusion. The following arrangement of stonefly habitats is based, therefore, only on obvious physiographical data.

The stonefly habitats can be primarily classified as running water and still water, and each of these can be subdivided as follows :—

Running Water.

1. *Trickles* (small trickles of water running from a spring or the end of a field drain, through the roots of *Juncus* and grass, among which dead leaves and other vegetable matter usually occur).
2. *Small stony streams* (becks) (small rapid streams such as are found in hilly and mountainous regions, and are anything from one to two feet to four or five yards across).
    - *a.* High streams (over about 1000 ft.).
    - *b.* Low streams (below about 1000 ft.).
        - i. Streams which dry up during drought.
        - ii. Streams which do not dry up.
3. *Stony rivers* (also typical of hilly and mountainous regions; small rivers ten to about thirty or more yards wide, with a stony or rocky substratum, and a rapid current).
    - *a.* Rivers or parts of rivers where the substratum is stable and covered with moss (*Fontinalis* and *Hypnum*).
    - *b.* Rivers or parts of rivers where the substratum is unstable and without any visible vegetation.
4. *Sluggish rivers* (large or small rivers or streams with a muddy bottom, and rooted vegetation).

Still Water.

1. *Stony shores of lakes* (typical of lakes in rocky regions) (Moon 1934).
    - *a.* Shores with large stones and boulders, little silt, and little or no rooted vegetation.
    - *b.* Shores with small stones, usually about fist size or slightly larger, some silt, and a *Littorella* or *Lobelia* sward covering most of the area between the stones (deltas and the drift shore described by Moon).

2. *The submerged parts of emergent vegetation of mountain pools (tarns) and small streams,* and similar localities where there is much vegetable matter.

The disadvantage of this classification is the overlapping of the various types of habitat; for instance, it is often difficult to decide whether some small bodies of running water should be referred to as trickles or small stony streams, and the edges of a sluggish river often have emergent vegetation, and therefore rank as still water. It is, however, convenient to have such a classification to which to refer. Within the stony habitats there is a number of micro-habitats, to which certain species are almost entirely confined. The most important of these micro-habitats are the leaf-packets in the small stony streams, and the moss in the stable regions of the rivers. Hora (1930) has discussed in some detail the micro-habitats in rapid running water, and of the micro-habitats mentioned by him three are of importance in stonefly ecology; these are the moss, the undersides of rocks, and the spaces between pebbles at the bottom of the river bed. In any body of stony running water or on any stony lake shore some or all of the following micro-habitats are present, and in them stonefly nymphs are found.

1. The moss on the top of the large stones and boulders. This is of greatest importance in stony rivers.
2. The undersides of large boulders and loose stones. This is the habitat in which the larger species usually live, and is typical of the rivers, larger streams, and unsilted stony lake shores.
3. The detritus and sand between the stones and gravel. This habitat occurs on all stony substrata even where the current is strong, because the larger stones shelter some parts of the bottom.
4. The packets of dead leaves and grass. This is a habitat typical of the small stony streams and trickles, and does not regularly occur in any other type of locality. The leaves are piled up on the upstream side of stones or roots.

Ecological studies on the fauna of running water in this country have been made by many workers, among whom may be mentioned Carpenter (1927 and 1928) and Percival and Whitehead (1929 and 1930), both of whom state that the nymphs of stoneflies are found on stony substrata in running water. Schoenemund (1924 and 1925b), Schwermer (1914) and Mertens (1923) have dealt in particular with the ecology of stoneflies, and their more detailed observations agree largely with observations made in the Lake District.

In the following section each species which has been obtained is dealt with separately, and the typical habitat of each is described and classified on the basis described above.

2. Habitats of the various species.

Perlodes mortoni.

Nymphs were found in twenty localities, seventeen of these being small stony streams, and three being stony rivers. This species was only once found above 1200 feet, one adult female being taken at 2000 ft. Of the small stony becks in which this species occurred nine were observed to dry up completely during drought, but in three of these, in which collections were made soon after the drought, large numbers of young specimens were found. In all localities the

nymphs were found under the larger loose stones. These observations are not quite in agreement with Mertens (1923), who states that the closely allied species *P. microcephala* (Pict.) occurs in almost all mountainous streams. Adults occur from March to July, being most common in April.

Dictyopterygella bicaudata.

Nymphs were found in fifteen localities, nine of these being stony lake shores with large stones and boulders; one of these lakes was in Caithness. Six of the localities were small stony streams above 700 ft. In none of the high mountain streams was the species found in company with *P. mortoni*, being always higher up the mountain-side than that species. Like the nymphs of *P. mortoni*, which they greatly resemble in form and feeding habits, those of *D. bicaudata* were always found under the larger stones. Miss Frost found this species several times in the River Liffey in Ireland, but always above 700 ft. On the lake shores the young specimens may be found on the smaller stones and gravel, but as they grow they migrate to the undersides of larger stones. This occurs in about October, and then the nymphs migrate slowly from the shore into deeper water, becoming difficult to find during December and January. In the spring they again return to shallower water, where they live for one or two months before emergence as adults. Mertens (1923) and Schoenemund (1924) both state that this species is a cold-water stenotherme, and this would seem to be supported by its rather peculiar distribution. Adults occur from April to July, being most common in April.

Perla (*Dinocras*) *cephalotes.*

Nymphs were taken in thirteen localities, ten of these being small stony streams, none of which dries up during drought, and three being stony rivers, one in Caithness. This species occurs right up to the sources, at 2000 ft., of the mountain streams in the Lake District, and is always much commoner in places where the substratum is stable and moss-covered. The higher parts of streams and rivers are often stable, and this may account for the statement by Percival and Whitehead (1929) that this species extends slightly higher into the hills than does *P. carlukiana*. Schoenemund (1924) states that it is more tolerant of mud than are the other species of the genus; it was not found in muddy localities in the Lake District. Adults occur in May and June.

P. (*Perla*) *carlukiana.*

Nymphs were found in fifteen localities, thirteen of these being small stony streams none of which dries up during drought, and two being stony rivers. In all these localities the nymphs were much commoner on unstable parts of the substratum, where they were found under the loose stones. The two rivers in which this species was found, the Brathay and the Rothay, which flow into the head of Windermere, show a marked contrast, the substratum of the Brathay being almost entirely stable and the species rare, whilst the substratum of the Rothay is largely unstable and the species so common that there are often several specimens under the same stone. Like *P. cephalotes*, this species is found right up to the sources of the mountain streams where the substratum is suitable. Adults occur in May and June.

Isoperla grammatica.

Nymphs were found in thirty-four localities, some of which are in Hampshire, and six of which were stony rivers, the rest being small stony streams, several

of which dry up completely every summer. The nymphs occurred under stones. In two of the Hampshire localities, the Allen River and the Till River, the substratum was sandy and light coloured, and from these localities the nymphs were very pale in colour (p. 487). Mertens (1923) and Schoenemund (1924) agree that this species is widely distributed on sandy or stony substrata in running water. The species was not taken above 1000 ft. Adults occur from April to August, being most common in May and June.

Chloroperla torrentium.

Nymphs were found in forty-seven localities, six of these being stony lake shores, the rest being various types of stony substrata in running water, and were recorded in several counties. The nymphs are to be found in most micro-habitats, but are most common under the stones and amongst the gravel and sand; they occur right up to the sources of the Lake District streams, and in streams which dry up completely during the summer. Adults occur from April to August, being most common in May.

C. tripunctata.

Nymphs were found in eleven localities, two of these being stony rivers, and the rest small stony streams which do not dry up during drought. Nymphs have been found in similar localities in Scotland and Ireland by Dr. Wingfield and Miss Frost respectively. Two nymphs were once found on a stony lake shore of Windermere, on which many other collections were made without finding the species; no specimens were found in any similar locality. The nymphs were always found among stones and gravel in the unstable parts of the beds of the streams and rivers; and no specimens were taken above 1200 ft. The reason for the absence of this species from streams which dry up during drought may be that, as indicated on p. 537, it probably takes two years to develop. Adults occur in May and June.

Taeniopteryx nebulosa.

Nymphs were taken in only one locality, the River Winster (WL); this is a sluggish river with rooted vegetation (*Myriophyllum*, *Hippuris*, and *Callitriche*) in which the nymphs appeared to be living. One specimen was also taken from a muddy dyke a few yards from the river. From the records of Lestage (1921) and Kühtreiber (1934) it appears that this species is found in similar localities in France and Austria, but Lestage also found it in moss on stones. Butcher, Longwell and Pentelow (1936) have recorded it from some reaches of the River Tees where there is a sandy and muddy substratum but no rooted vegetation. Apparently the nymphs are always coated with mud. Adults occur from February to April.

Brachyptera risi.

Nymphs were common in fourteen localities, all of these being small stony streams, some of which dry up during drought. Occasional specimens were also found in the moss in two stony rivers, the Rothay and the Brathay, which were frequently visited, and Miss Frost found the species to be present in the moss in the River Liffey in Ireland. In the streams the nymphs were always found under stones. It seems that this species extends some way up into the hills, as adult specimens were taken at 1400 ft. Mertens (1923) says that it is found in small cold streams, and Schoenemund (1924) says that nymphs of this

genus inhabit the more sheltered places in rivers. It is possible that the rapid current in the Lake District rivers is the factor which prevents it from living in them. Adults occur from March to July.

Capnia nigra.

Nymphs were found only on the slightly silted stony shores of Windermere, and adults were taken near similar localities in Ennerdale Water and Ullswater. Adults have been recorded from the shores of several rivers in Britain; and nymphs of the genus are recorded from the River Tees (Butcher, Longwell and Pentelow, 1936), and from the River Liffey by Miss Frost; these latter may, however, belong to one of the other two species on the British list. No nymphs were found in running water in the Lake District. Adults occur from February to May, and on the shores of Windermere are commonest during March.

Leuctra geniculata.

Nymphs were found to be common in only four localities in the Lake District, and two in Hampshire; these were all rivers or large streams with stony substrata, which do not dry up during drought, and which are always at least one foot deep. Two isolated specimens were taken from a slightly silted stony shore of Ullswater. Lestage (1920) says that this species lives on the underside of large deeply embedded stones and boulders in fairly deep water, and this has been found to be true of specimens over about 6 mm. in the Lake District; smaller specimens live among the stones and gravel. Lestage has suggested that the peculiar processes on the antennae are connected with the burrowing habit, and they certainly do appear at about the size at which the nymph starts to burrow; it is possible that they enable the nymph to worm its way down between the stone surface and the underlying coarse sand and gravel. Adults occur from August to November, and are commonest in late August and early September; there are two isolated records of adults of this species earlier in the year.

L. nigra.

Nymphs were found in seventeen localities in the Lake District, fifteen of these being small stony streams, several of which dry up during drought, and two being silted stony shores of Windermere; one specimen was taken in a small stony beck at 2000 ft., and one in a sluggish river. Adults were taken at 1400 ft. The nymphs were always found in silty localities such as the small pools in the streams or in the leaf-packets; indeed where there is a great quantity of the latter material the species is extraordinarily abundant. Its absence from the stony rivers of the Lake District is possibly explained by the fact that in these rivers the current is too strong to allow the accumulation of much dead vegetable matter and detritus. Kühtreiber (1934) mentions similar habitats of this species in Austria, and says that it extends up the mountains to the sources of the streams, being most common in woodland streams on mountain sides. Adults occur from February to June, being most common in April.

L. inermis.

Nymphs were found in twenty localities in the Lake District, two of these being stony rivers, and eighteen small stony streams. Several of these streams dry up during severe drought, but the species is absent from streams which are dry early in the summer. Nymphs were found right up to the sources of

streams over 2000 ft., and were usually among the stones and gravel. These observations agree with those made by Kühtreiber (1934) in Austria. Adults occur from March to August, being commonest in May and June.

L. fusciventris.

Nymphs were found in thirty localities in the Lake District, representing all types of water with a stony substratum, and were also found in similar localities in Caithness and Perthshire. The species occurred early in the summer in several small stony streams which dry up completely during drought, but was absent from these after the dry period. It is very abundant, and it seems that these streams are recolonised every year, the nymphs being killed by the drought. The species occurs right up to the sources, at 2000 ft., of the mountain streams in the Lake District, and is usually found among the smaller stones and gravel. Schoenemund (1924) states that it lives in the sheltered parts of rivers. Adults occur from June to November, being commonest in July, August, and September.

L. hippopus.

Nymphs were found in thirty-two localities in the Lake District, two of these being the stony shores of lakes, three being stony rivers, and twenty-seven being small stony streams, many of which dry up during drought. They were also obtained from the River Forss in Caithness, and Miss Frost found the species to be common in the River Liffey in Ireland. The occurrence of this species on the stony shores of lakes is of interest in that while the nymphs were common in Derwentwater and Bassenthwaite, and adults were found on an island in Ennerdale Water, the species is absent from the shores of Windermere and Esthwaite Water, except just at the mouths of streams and rivers in which it is often abundant; no explanation is offered for this. The nymphs live among stones and gravel, and in leaf-packets when these are present, and occur right up to the sources, at 2000 ft., of streams in the Lake District. Kühtreiber (1934) says that the species is found in the middle reaches of mountain streams, being absent from the head waters, but mentions also that it may be found in almost stagnant water. Schoenemund (1934) found it in the more sheltered parts of rivers. Adults occur from February to June, being commonest in March and April.

L. moselyi.

Nymphs were found in only three small stony streams in the Lake District, none of which dries up completely even during severe drought, and one of which rises at 2000 ft., the species being found right up to its source. Adults were taken on the wing near two similar high streams. One of the two other streams, the sources of both of which are below 800 ft., in which the species was abundant in the summer of 1939 and the spring of 1940, was so reduced during the severe drought of the summer of 1940 that only a series of small pools was left along its course. The species survived in these pools, but was greatly reduced in number, thus showing that it is unable to withstand complete drought. Adults occur in July and August.

Protonemura meyeri.

Nymphs were found in nineteen localities in the Lake District, two of these being stony rivers, and the rest small stony streams; several of the latter dry up during drought. In the rivers they were entirely confined to the moss on stable parts of the substratum, but in the streams they occurred under stones,

in leaf-packets, and in any moss that was present. Miss Frost found them to be common in moss in the River Liffey in Ireland. It is possible that the greater current in the rivers is the reason why they take refuge in the moss, which also forms a readily available food-supply. The species occurs right up to the sources of streams at 2000 ft. in the Lake District, and Miss Frost records it from the sources of the River Liffey at 1800 ft. Schoenemund (1934) states that it is found in Germany in the moss of the rivers. Adults occur from February to July, being commonest in March, April and May; a few specimens have been recorded in August and September at high altitudes.

P. praecox.

Nymphs were found in eleven small stony streams in the Lake District, four of which dry up during drought. Four specimens were also found in the moss from stable parts of the substratum of the River Rothay; from this habitat several hundred specimens of *P. meyeri* were taken during the course of a year. Ordinarily the species lives under stones and in leaf-packets in the small streams; it occurs up to the sources of streams at 2000 ft. in the Lake District. This is in agreement with the observations of Schoenemund (1924), Kühtreiber (1934), and Mertens (1923). Adults occur from February to May, being commonest in March and early April.

Amphinemura cinerea.

Nymphs were found in twenty-six localities in the Lake District, two of these being stony rivers, one a trickle, and the rest small stony streams. The distribution of this species is peculiar. In the high stony streams and in the stony rivers it is abundant, as it is in the lower parts of streams which rise at a high altitude; in lowland streams, however, it is absent or only present in small numbers, unless these streams are the outflows of bodies of still water. It is possible that this is the result of the drying up of streams, because the high streams, rivers, and outflows never dry up, and are always clear running water, while the lowland streams, even if they do not dry up, become very low during the summer, and the bottom becomes much silted. The one trickle in which it was found flowed straight into an outflow in which the species was common, and was probably regularly recolonised from there. Butcher, Longwell, and Pentelow (1936) state that this species is more tolerant of acid water than many animals. The nymphs are always covered with flocculent detritus which adheres to the long bristles on the abdomen, but they are not found in particularly silty localities; the usual habitat is among stones and gravel, but they are also found in moss when this is present. Adults occur from April to August, but are commonest in May, June and July.

A. standfussi.

Nymphs were found only in one small stony stream forming the boundary between S. Hants and Dorset. Collections were made there in May (by T. T. Macan), December (by N. Hynes), and April (by J. W. Jones); in all these collections the nymphs were found in leaf-packets, which are common in the stream. A considerable amount of silt was present, and it appeared that the stream did not dry up during drought. Adults occur in May and June, and there is one record in July.

Nemoura erratica.

Nymphs were common in only one small stony stream in the Lake District, two specimens being taken in streams at high altitudes, and one adult being

recorded at 1500 ft.; one specimen was also taken in a lowland stream about one mile from the first locality. The stream in which the species is abundant is only two or three feet wide, dries up regularly every year, and flows through a wood to the shore of Windermere. It is full of dead leaves and twigs, and amongst these the nymphs were found in large numbers. They were absent from several similar streams in the neighbourhood. Adults occur from February to June, but are commonest in March.

N. cambrica.

Nymphs were found in thirty localities in the Lake District, three of these being trickles, and the rest small stony streams, many of which dry up completely during drought; three specimens were also taken near the banks of two stony rivers. This species, which is often extraordinarily abundant, occurs up to 1400 ft., but has not been found above that altitude. It is most abundant where there is much decaying vegetable matter, and is a typical inhabitant of leaf-packets. Where, as in most of the higher streams and in the rivers, leaf-packets do not develop, the species is absent or rare. Adults occur from April to June, being commonest in April and early May.

N. avicularis.

Nymphs were found in seventeen localities in the Lake District, thirteen of these being stony lake shores, two sluggish rivers in which the species occurred in rooted vegetation (*Callitriche*), one the outflow of a lake, Esthwaite Water, in which the species is very abundant, and one the sheltered bays and pools of a stony river, where rooted vegetation and thick moss had developed. In the lakes the species is always most abundant where the stones are small and silted, and *Littorella* and similar plants are present. Morton (1894) describes this species as lacustrine. Adults occur from March to June, being commonest in April and May.

N. variegata.

Nymphs were found in nine localities in the Lake District, two of these being trickles, four the submerged parts of the emergent vegetation (*Carex*) of fish ponds (tarns and lochans), and two the submerged grass and similar vegetation on the banks of sluggish streams; one of the fish ponds is 1800 ft. above sea-level. Outside the Lake District this species has been taken in the submerged grass and leaf-packets in clean ponds and streams in Surrey and Hampshire. In one small Surrey stream the species was observed to be annihilated by continuous drought. These observations agree with those of Mertens (1923), Schoenemund (1924), and Kühtreiber (1934). Adults occur from March to July.

Nemurella inconspicua.

Nymphs were taken in many places in the Lake District, including the submerged parts of emergent vegetation in fish ponds, swamps, cattle ponds, trickles, silty pools in small becks or adjoining them, the submerged grass in slow streams, the extreme head waters of mountain streams where grass and moss hang into the water, and the very sheltered bays in lakes where large accumulations of dead leaves collect. The species therefore seems to need for its existence slow running or still water and much vegetable matter. These observations are in agreement with those of previous authors (Schoenemund, 1924, and Kühtreiber, 1934). Adults occur from March to September.

The habitats of stonefly nymphs and the species which normally occur in them can therefore be tabulated (fig. 19). The factors controlling the distribution of the various species within these habitats are discussed later (p. 542).

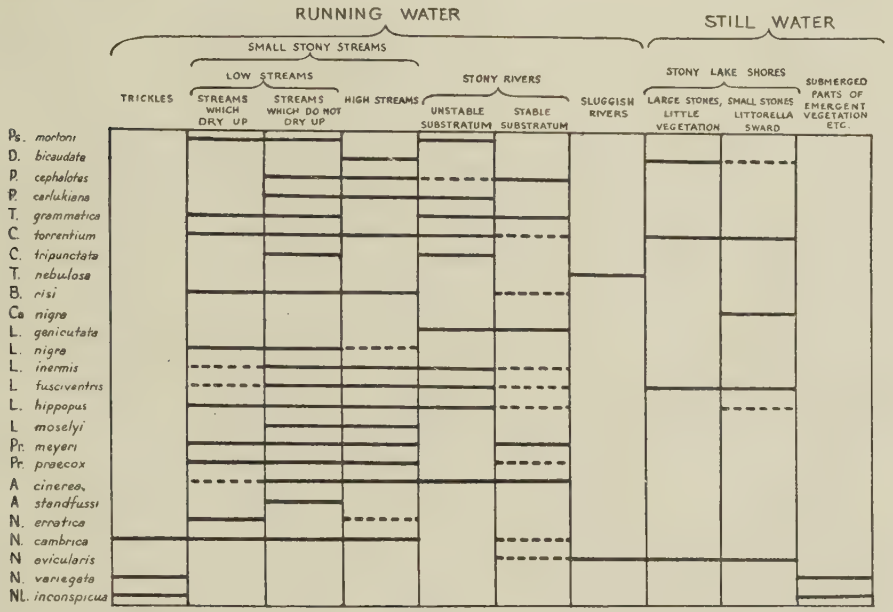

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Fig. 19.—The habitats of the species.

The continuous lines indicate the habitats where the nymphs are common, and the dotted lines those where they are only occasionally found.

3. Feeding habits.

The feeding habits of twenty-three species have been investigated and the results obtained have been tabulated (table 1). In this table the number of specimens in which any given foodstuff has been found is given, and beside it in brackets is the percentage of the total number of nymphs examined. The nymphs were collected in the field and killed there, or shortly after arriving back at the laboratory, by placing them in 2% formaldehyde. The gut contents were then extracted and examined under the microscope. The method of extraction of the gut contents varied according to the family to which the nymphs belonged. In the Perlodidae and Perlidae the fore gut is heavily chitinised and tough, and has posteriorly a circle of inwardly directed hooks, which prevent large food particles from passing into the mid gut. In these families the intersegmental membrane of the neck was cut round and the head pulled; the gut then broke off just below the circle of hooks and was pulled out, transferred to a slide, and cut longitudinally for extraction of the contents. The contents of several mid and hind guts were examined but no large food particles were found in them; it was assumed therefore, as indicated by Grau (1926), that in these families the larger food particles are regurgitated after digestion, and consequently that the contents of the mid and hind guts do not completely represent the food of the nymph. In the Taeniopterygidae,

TABLE

Table showing the number of nymphs of each species examined for gut contents, and the corresponding percentages of

Species	*P. mortoni*	*D. bicaudata*	*P. cephalotes*	*P. carlukiana*	*I. grammatica*	*C. torrentium*	*C. tripunctata*	*B. risi*	*Ca. nigra*	*L. geniculata*
Number of specimens examined	111	41	105	128	253	146	45	66	26	54
Vegetable and Mineral Matter: Diatoms	24(22)	4(10)	10(10)	46(36)	83(33)	50(34)	15(33)	40(61)	21(81)	15(28)
Filamentous green algae	23(21)	2 (5)	30(29)	43(34)	82(32)	45(31)	7(16)	5 (8)	11(42)	21(39)
Desmids	1 (1)	—	2 (2)	2 (2)	30(12)	13 (9)	1 (2)	—	—	15(28)
Chantransia	4 (4)	—	2 (2)	16(13)	15 (6)	3 (2)	6(13)	—	—	—
Other algae	7 (6)	1 (2)	1 (1)	—	10 (4)	7 (5)	3 (7)	29(44)	—	19(35)
Higher plant and moss tissue	14(13)	3 (7)	10(10)	8 (6)	20 (8)	28(19)	12(27)	12(18)	10(38)	52(96)
Detritus and undetermined matter	5 (5)	6(15)	4 (4)	3 (2)	17 (7)	59(40)	15(33)	35(53)	13(50)	53(98)
Mineral matter	1 (1)	2 (5)	1 (1)	—	6 (2)	19(13)	4 (9)	22(33)	6(23)	44(81)
Number of specimens with only vegetable and mineral matter	11(10)	4(10)	4 (4)	20(16)	26(10)	53(36)	13(29)	66(100)	26(100)	43(80)
Animal Matter: Protozoa	—	—	3 (3)	—	1(<1)	1 (1)	—	—	—	—
Nematodes	1 (1)	—	—	1 (1)	1(<1)	3 (2)	—	—	—	—
Rotifers	—	1 (2)	2 (2)	—	9 (3)	20(14)	2 (4)	—	—	—
Oligochaetes and leeches	1 (1)	4(10)	3 (3)	1 (1)	5 (2)	1 (1)	—	—	—	—
Crustacea	3 (3)	6(15)	2 (2)	3 (2)	8 (3)	8 (5)	—	—	—	2 (4)
Terrestrial arthropods	3 (3)	1 (2)	2 (2)	—	2 (1)	—	—	—	—	—
Plecoptera nymphs	14(13)	9(22)	25(24)	20(16)	23 (9)	3 (2)	3 (7)	—	—	3 (6)
Ephemeroptera nymphs	57(51)	5(12)	27(26)	50(39)	45(18)	10 (7)	11(24)	—	—	1 (2)
Trichoptera larvae	9 (8)	5(12)	10(10)	4 (3)	3 (1)	2 (1)	2 (4)	—	—	—
Chironomid larvae	52(47)	20(49)	42(40)	34(27)	148(58)	36(25)	13(29)	—	—	2 (4)
Simulium larvae	13(12)	2 (5)	4 (4)	6 (5)	22 (9)	2 (1)	—	—	—	—
Unidentified and other insect remains	14(13)	11(27)	32(30)	23(18)	47(69)	35(24)	10(22)	—	—	9(17)
Hydrachnids	—	2 (5)	—	2 (2)	—	—	—	—	—	—
Number of specimens with only animal matter	62(56)	28(68)	67(64)	64(50)	117(47)	30(21)	10(22)	—	—	—
Number of specimens with mixed animal and vegetable matter	38(34)	9(22)	34(32)	44(34)	110(43)	63(43)	22(49)	—	—	11(20)

CAPNIIDAE, LEUCTRIDAE, and NEMOURIDAE the fore gut, like the mid and hind gut, is soft, and there is no structure preventing the larger food particles from passing through to the anus. In these families the head was cut off and the contents of the fore gut were squeezed out on to a slide for examination. Usually none of the gut itself came out with the food, but when it did it was easily recognised under the microscope.

An inspection of table 1 will show that while the PERLODIDAE and PERLIDAE feed on mixed animal and vegetable matter, the other families feed almost entirely on plant material. In these latter families it is almost certain that the undetermined matter and detritus was the product of decaying leaves and similar material, because it was always found in company with pieces of undoubted higher plant tissue which it greatly resembled in general appearance. Several specimens of these primarily herbivorous families contained animal matter, and it is noticeable that this was very often the cercal or antennal joints of plecopteran nymphs. These were certainly not parts of the nymphs being examined, because great care was always taken to remove any accidentally

1.

number of specimens in which each class of foodstuff was found. The figures in brackets are the total number examined.

L. nigra	*L. inermis*	*L. fusciventris*	*L. hippopus*	*L. moselyi*	*P. meyeri*	*P. praecox*	*A. cinerea*	*N. erratica*	*N. cambrica*	*N. avicularis*	*N. variegata*	*N. inconspicua*
68	122	104	202	34	59	43	98	91	151	86	53	52
4 (6)	18(15)	7 (7)	9 (4)	—	10(17)	4 (9)	26(27)	1 (1)	11 (7)	18(21)	6(11)	1 (2)
1 (1)	6 (5)	8 (8)	4 (2)	—	3 (5)	2 (5)	14(14)	—	3 (2)	3 (2)	6(11)	6(12)
—	4 (3)	—	—	—	1 (2)	1 (2)	2 (2)	—	—	1 (1)	—	—
—	—	—	2 (1)	—	3 (5)	—	2 (2)	—	—	—	—	—
1 (1)	3 (2)	1 (1)	2 (1)	—	—	3 (7)	2 (2)	1 (1)	13 (9)	—	5 (9)	—
59(87)	102(84)	97(93)	182(90)	33(97)	56(95)	42(98)	62(63)	90(99)	127(84)	82(95)	47(89)	43(83)
56(82)	100(82)	97(93)	125(62)	33(97)	6(10)	5(12)	69(70)	5 (5)	32(21)	28(33)	7(13)	18(35)
41(60)	87(71)	89(86)	107(53)	30(88)	1 (2)	4 (9)	1 (1)	3 (3)	22(15)	28(33)	4 (8)	22(42)
68(100)	122(100)	96(92)	199(98)	30(88)	59(100)	43(100)	98(100)	90(99)	151(100)	84(98)	50(94)	47(90)
—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	8 (8)	2 (1)	1 (3)	—	—	—	1 (1)	—	2 (2)	3 (6)	5(10)
—	—	—	—	1 (3)	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	1(<1)	2 (6)	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	8 (8)	3 (2)	4(12)	—	—	—	1 (1)	—	2 (2)	3 (6)	5(10)

detached fragments of the nymphs after dissection, and because the antennal and cercal joints were always clearly mixed with the rest of the gut contents. It seems that nymphs of these families, when feeding on the decaying higher plant tissue and detritus on which they normally live, will eat any dead animal matter with which they come into contact, and, as the cast skins of stonefly nymphs are common in places where many stoneflies are living, these are frequently eaten. Some evidence of this tendency to eat dead animal matter has been obtained. When nymphs of the species *Nemurella inconspicua*, *Nemoura avicularis* and *N. variegata* were being reared to maturity in the laboratory, several adults and cast nymphal skins fell into the water and were left there for one or two days. When examined later these adults and skins were often found to have been almost entirely eaten, only the wings and the hard parts of the thorax and genitalia remaining. Similarly the presence of terrestrial arthropods, among which were spiders, Nematoceran Diptera, and Caddis flies, in the guts of several specimens of the PERLODIDAE and PERLIDAE indicate that these families also eat dead animal matter. These families do,

however, also eat living animals, and it is probable that this is more usual. Specimens of *Perlodes*, *Dictyopterygella*, and *Perla* have been seen to eat ephemeropteran nymphs in the laboratory. They did not appear to be able to see these nymphs, but as soon as they came into contact with the antennae or cerci they pounced on them, worrying them as a dog worries a rat, after which they were eaten quickly. It was noticed that after a nymph of any of these large species has eaten, it jerks itself up and down on its legs. This movement always occurs if the nymphs are kept for some time in still water, and Schoenemund (1925b) has suggested that it is done in order to make the water rush over the gills or heavily tracheated intersegmental membrane, and so to facilitate oxygen exchange in water in which the concentration of oxygen is falling. But this cannot explain why it is done after feeding, because nymphs have been seen to do it in running water in the laboratory, and only those specimens which had been fed were observed to act in this way.

Specimens from as many localities and in as many stages of development as possible were selected for examination of gut contents, because it was found that there was some variation in the food of the same species from various localities. Except in *Isoperla grammatica*, however, the type of food was not found to vary from place to place. Usually from about 50% to 90% of the specimens collected had no food in their guts, so it seems that the nymphs do not feed continuously. It often took specimens in the laboratory two or three days to empty their guts; so this high percentage of empty guts is not an indication that the feeding is done at night. That the Perlodidae and Perlidae feed at night is, however, indicated by the composition of the gut contents. The nymphs are never seen on the upper sides of stones during the day, but the guts often contained enormous numbers of algae which presumably were collected on the tops of stones, because algae are not usually abundant in the dark on the under sides. This is in agreement with the statement by Hubault (1927) that the stream fauna comes out on to the tops of stones at night.

It will be convenient to consider in more detail the various classes of food-stuffs, and the feeding habits of each family.

The algae found in the guts represented many genera. The most common diatoms were *Ceratoneis*, *Cymbella*, *Tabellaria*, *Gomphonema*, *Amphora*, *Synedra*, *Fragillaria*, *Achnanthes*, *Cocconeis*, *Pinnularia* and *Navicula*, *Cocconeis* being the commonest genus in the Leuctridae and Nemouridae. Among the filamentous green algae, common genera were *Zygnema*, *Ulothrix*, and *Oedogonium*, but several other unidentified genera were also present; these could not be identified because of the altered state of the cell contents. The desmids were all species of *Cosmarium*, *Staurastrum*, and *Closterium*. The term *Chantransia* has been used for all the branched filamentous red algae found in the guts. Small spores were seen on several of these, but it is probable that many were the young stages of *Lemanea*, which is common in many of the streams. Other algae were forms such as *Gongrosira* and other unidentified encrusting algae, and many free-living genera such as *Ankistrodesmus*, *Pediastrum* and *Scenedesmus*; a few blue-green algae were also present. The higher plant and moss tissue was usually in the form of small pieces containing from two or three to several cells, and often in a state of decomposition. It was not always possible to decide whether these were pieces of higher plants or moss, so they have been classed together. With this latter material large quantities of similar matter were often present, but it was so finely divided that no structure could be made out; this has been called detritus and unidentified matter,

although it seems almost certain that a large part of it is really finely divided and much decayed higher plant tissue. That its finely divided state is not entirely due to its having been eaten by the nymph is shown by the frequent occurrence with it of sand particles (mineral matter), which can hardly have been selected as food, but which would be unavoidable when mixed with detritus. This mixture of sand and detritus is presumably the brown flocculent material which is found in sheltered places in streams and on stony lake shores.

The animals found in the guts represented most groups of aquatic insects occurring with stonefly nymphs. Beetle larvae were, however, rare, although Grau (1926) found them in the guts of *Perla bipunctata* nymphs. The Protozoa, which were only rarely found, were colonial vorticellids; it is possible that these are eaten more frequently than these investigations suggest, but soon become unrecognisable in the guts. The same applies to the Nematodes, Rotifers, Oligochaetes, and leeches, some of which were difficult to recognise. The Crustacea were chiefly Cladocera and *Gammarus*, the latter always being broken up but recognisable because of its appendages. Plecoptera nymphs (chiefly Leuctridae and Nemouridae), Ephemeroptera nymphs (chiefly *Baëtis* and Ecdyonurids), and Trichoptera larvae were common, and, although usually broken up, could be recognised by the tarsi and cercal joints; often only part of one of these animals was present in the gut. Chironomid and *Simulium* larvae were easily recognised by their head capsules, which often occurred in large numbers; over 100 chironomid larvae were once found in the gut of a *Perlodes* nymph. Unidentified insect remains usually consisted of small pieces of chitin, and with these have been classed such insects as beetle and Tipulid larvae, which were found only rarely. The small pieces of chitin may have formed part of insects belonging to any of the previous groups.

Perlodidae.

The two species investigated, *Perlodes mortoni* and *Dictyopterygella bicaudata*, show a similar diet, and feed largely on animal matter, but also eat algae and higher plant tissue. *D. bicaudata* from the high streams sometimes contained *Simulium* larvae, and in those from lake shores occasional Cladocera were present. This is an indication that no great selection of foodstuffs occurs, anything which is available being eaten, because *Simulium* is confined to running water, and Cladocera are absent from the high streams. In both species the smaller specimens were found to have eaten smaller animals than the larger specimens, and this involves in most localities a change as the nymph grows from an animal diet of chironomid larvae to ephemeropteran nymphs. Previous workers have stated that *Perlodes* is almost entirely carnivorous, but this is disproved by the fact that 10% of the specimens examined contained only vegetable and mineral matter. The mineral matter, which was sand, must have been eaten accidentally.

Perlidae.

The feeding habits of *Perla* were found to be similar to those of the Perlodidae, and there was no marked difference between the diet of the two species, except that fewer specimens of *P. cephalotes* had eaten only vegetable matter. Grau (1926) states that *Perla* is more essentially carnivorous than *Perlodes*, but this does not seem to be true of the British species. *Isoperla grammatica* has a similar diet, but specimens from small streams are much more carnivorous than those from stony rivers; of 87 nymphs examined from a small stony stream

(Boathouse 2 Beck) 62 (71%) had eaten only animal matter, 20 (23%) both animal and vegetable matter, and 5 (6%) only vegetable matter, while from a stony river (R. Rothay) of 113 specimens examined, the numbers were 23 (20%), 73 (64%), and 17 (16%) respectively. The reason for this tendency of the species to eat more animal matter when living in small streams may be the greater concentration of animals there, or that the algae are less numerous than in the rivers, because a large part of the bottom becomes covered with dead leaves. This difference in feeding may account for the difference in growth rate shown by this species in the two localities (p. 540). The two British species of *Chloroperla* show similar feeding habits to the other species in the family, except that smaller animals are eaten, and there is a greater tendency to eat detritus, which is presumably the product of decaying leaves.

Taeniopterygidae.

Only one species, *Brachyptera risi*, of this family, was investigated, and the gut contents of many specimens proved extremely difficult to identify. No animal matter was present, and there were often isolated pieces of higher plant tissue. The rest of the gut contents was often obscure. Pieces of algae, classed here as "other algae," were probably such forms as *Gongrosira*, and nearly all the diatoms were *Cocconeis*. This indicates that the species feeds largely on scrapings from stones, as both *Gongrosira* and *Cocconeis* are epilithic algae. Sand and finely divided detritus were also often present and these may have been entangled with the algae on the stones. It is possible that this feeding habit is correlated with the presence of a complex comb of bristles on the tip of the galea (fig. 2D), which may be the organ with which the scraping is done. Lestage (1921) suggests, from an inspection of the mouth-parts of the nymph, that *Taeniopteryx nebulosa* is carnivorous, but this seems improbable, because the mouth-parts are similar to those of the herbivorous Nemouridae, and quite unlike those of the more carnivorous forms. It seems probable that this species feeds on the plants among which it lives. It certainly would not be able to scrape stones, because stones are not usually present in its normal habitat, and it is noticeable in this connection that the tip of the galea is simple.

Capniidae.

Unfortunately it was possible to examine the gut contents of only 26 nymphs of *Capnia nigra*, but these show that only vegetable matter is eaten and that algae and higher plant tissue form a considerable part of the diet. As in other families, the detritus, among which many sand grains were usually visible, appeared to be the product of decaying leaves. The great majority of the diatoms present belong to the genus *Achnanthes*.

Leuctridae.

The six British species of *Leuctra* show a very uniform diet, consisting of higher plant tissue, the detritus resulting from its decay, and sand particles, which presumably get mixed up with the detritus and are eaten with it. Algae occurred in many specimens, but never made up an important part of the gut contents; the diatom most frequently present was *Cocconeis*, which may have been growing on the higher plant tissue or have fallen among the detritus. *L. geniculata* showed a far greater proportion of algae than the other species;

these were chiefly filamentous green algae of various genera, members of the Chlorococcales such as *Scenedesmus* and *Pediastrum*, and the desmid *Staurastrum*. It is possible that such algae are more readily available in the moss on the stones under which this species usually lives, than among the smaller stones and gravel where the other species usually occur. Several specimens of this genus, particularly in the species *L. geniculata*, contained small amounts of animal matter but, as explained above, it seems that these are eaten only when found dead, or are taken into the mouth among the detritus as are the sand particles.

Nemouridae.

This family also shows great uniformity in feeding habits, but unlike the last, there is, in most species, less tendency to feed on the detritus produced by the decay of dead leaves, the dead leaves themselves being more often eaten. Several of the species inhabit leaf packets, and presumably chew off pieces of the leaves. Algae of all kinds are eaten also, but rarely form an important part of the gut contents. *Protonemura meyeri* is common in the *Fontinalis* on the tops of large stones in the stony rivers, and specimens from such localities were found to have fed almost entirely on the moss; occasional filamentous algae and diatoms were present, however, and these presumably were growing on the moss. Specimens of *Amphinemura cinerea* contained much more detritus than the other species of the family, but unlike species of *Leuctra*, sand was usually absent. This may be because the species lives among the moss on the stones, and among the smaller stones on the beds of stony rivers, where the current is too swift to allow sufficient detritus and leaves to collect and entangle particles of sand. Specimens of *Nemoura variegata* have been kept for months in the laboratory on a diet of dead *Carex* leaves, and have grown and emerged as adults. The gut contents of specimens of this species varied with the locality; in *Carex* beds, where algae grow profusely, algae were found in the guts; but in trickles, where almost the only vegetable matter is dead leaves, higher plant tissue was the chief diet. The feeding habits of *Amphinemura standfussi* were not investigated, but it seems likely that its food is similar to that of the other species of the family; nymphs lived and grew to maturity in the laboratory on a diet of dead oak leaves.

Schoenemund (1924) says that the early instars of stoneflies feed on fine detritus. The first instar larvae of several species were seen to eat any finely divided material which was given to them. Those of *Capnia nigra* ate planktonic algae, and those of *Nemoura erratica* ate finely powdered dog biscuit. It seems, therefore, that the detritus, which forms so important a part of the food of the older nymphs, is the diet of the early stages.

Many workers have stated that the larger stonefly nymphs are entirely carnivorous, but it can be seen from the results given here that all species eat a considerable amount of vegetable matter, and that the dead leaves of terrestrial plants are the chief source of food for most of the smaller species. In the high streams where the leaves of trees are absent, dead grass and plants fulfil the same function.

4. Length of life and growth.

Many of the earlier workers supposed that stoneflies passed through their entire life-cycle in one year. Later, Mertens (1923), Schoenemund (1925b), and others concluded that some of the larger genera take longer than one year,

and it became generally agreed that *Perla* takes three years and *Perlodes* two. Slightly smaller forms such as *Dictyopterygella bicaudata* were stated to take one year to complete their cycle, as were all the small species. Ris (1902) claims that *Nemoura variegata* and *Nemurella inconspicua* have two generations every year, but Schoenemund (1924) concludes that these species have only a long emergence period.

During the present work, an attempt has been made to test the correctness of some of these statements. *Perlodes*, *Dictyopterygella*, *Perla*, and most of the genera of small stoneflies were watched closely in the field, and it appears that, although there is some doubt in the case of *Chloroperla tripunctata*, all species except *Perla* spp. show a one-year growth cycle. Schoenemund mentions finding half-grown nymphs of *Perlodes* just after the adults had emerged, but this was never seen in the Lake District. As, however, there was doubt as to the length of life of *Perlodes* and *Perla*, it was decided to analyse collections of the nymphs to find the distribution of the sizes within a natural population. Accordingly, collections of each of the three British species in these two genera were made in localities where they were known to be common. During these collections, every nymph found was taken, and because of the care required to eliminate selection of the size groups, due to the greater ease with which the larger specimens could be found, it was not possible to obtain very large samples. The samples are, however, large enough to be examined statistically. The length, from the front of the head to the base of the cerci, of the nymphs, was then measured, and the lengths arranged in frequency classes. These were at 1-mm. intervals in both species of *Perla*, of which collections were made in May, just before the adults were emerging, and at $\frac{1}{2}$-mm. intervals in *Perlodes mortoni*, of which collections were made in October, about half-way between two emergence periods, when the population was much more uniform than in *Perla*. These figures have been plotted as histograms (fig. 20), and from these it can be seen that the nymphs of both species of *Perla* fall into three main size groups, while those of *Perlodes* show only one main group. The figures for the latter species were tested by the χ^2 method, and χ^2 was found to equal 6·287, with six degrees of freedom. The corresponding value of P is about 0·45. The data do not show a significant misfit from the best-fitting normal distribution. It may be assumed therefore that the lengths form a homogeneous unimodal group, and that *P. mortoni* takes only one year to complete its life-cycle in Britain. This is borne out by field observations.

The figures for *Perla* indicate, however, that both species have a three-year cycle, because the hatching period is short, and the smaller nymphs would not have had time to grow to their full size before the end of June, when this period ends. The last-year group in each species seems to show a bimodal distribution, and this is probably due to the difference in size between the sexes of the full-grown nymphs. The figures for the last two-year groups of *Perla carlukiana* have been subjected separately to the χ^2 test. The third-year group gives a value for χ^2 of 26·23, with eight degrees of freedom, and this gives, as would have been expected, a probability of more than 999 to 1 that the best-fitting normal population would not give so bad a fit. The second-year group, however, gives a value of 3·98 for χ^2 with five degrees of freedom, giving a value of P of about 0·55. It thus seems reasonable to assume that the samples of lengths are from a normal distribution. Although the number of specimens in this latter-year group is small, the likelihood that it represents a population normally distributed as to length is such that it can be said with a considerable chance of accuracy that two-year-old specimens do not show the marked size difference

between the sexes that is shown by the full-grown nymphs, and that this difference appears during the third year of life. Something similar must occur during the last four months of nymphal life in *P. mortoni*, because there is a marked size difference between the sexes of the full-grown nymphs, and as shown above, this difference is not apparent in half-grown specimens.

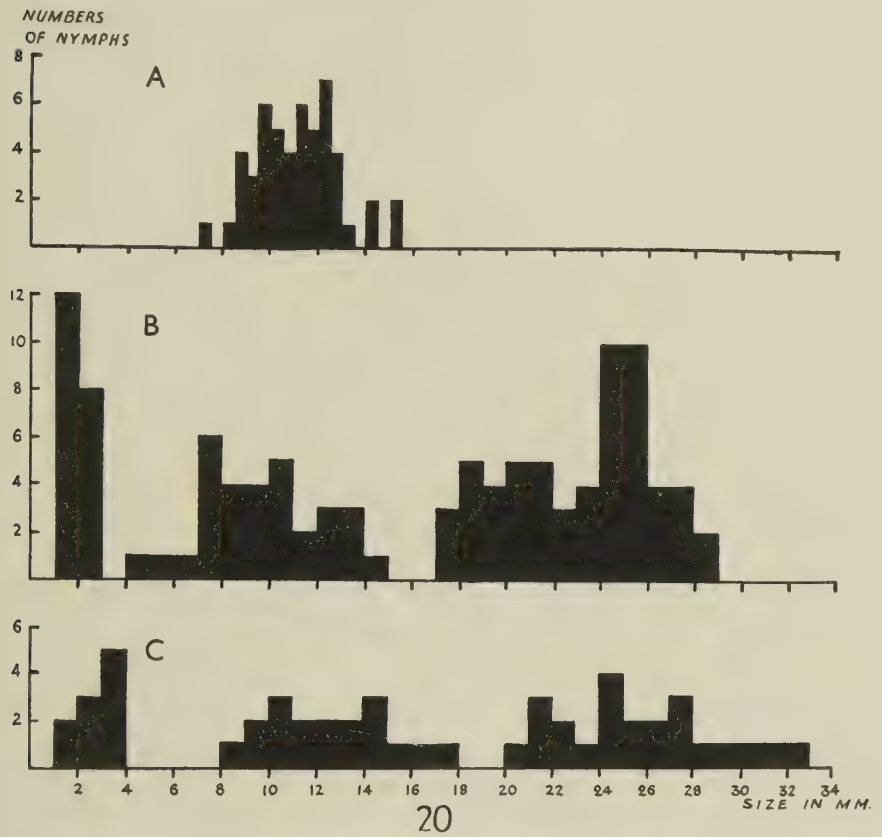

Fig. 20.—Histograms showing the distribution of size groups in large collections of nymphs. The number of specimens is plotted against frequency classes at 0·5- or 1·0-mm. intervals.

A, *Perlodes mortoni*, collection of 51 specimens from WL, Hawkshead, How Beck, 5.x.1940 (*Hynes*), placed in frequency classes at 0·5-mm. intervals; B, *Perla carlukiana*, collection of 110 specimens from WL, R. Rothay, 23–25.v.1940 (*Hynes*), placed in frequency classes at 1-mm. intervals; C, *P. cephalotes*, collection of 52 specimens from WL, R. Rothay and R. Brathay, 23–25.v.1940 (*Hynes*), placed in frequency classes at 1·0-mm. intervals.

All other species, with the exception of *C. tripunctata*, were found to complete their life-history in one year, because for all species there was a period of two or three months after the adults had emerged, during which no nymphs, or, in *N. variegata* and *N. inconspicua*, only very small nymphs, could be found. Nymphs of *C. tripunctata*, however, were found during most months, and in May, shortly after the adults had appeared, specimens from $2\frac{3}{4}$ to $5\frac{1}{2}$ mm. were found. These were too large to have hatched from eggs laid by the adults during that month, and, being less than half-grown, could not emerge as adults

before the end of June, which is the end of the flight period (Hynes, 1940). This indicates that the species takes more than one year to complete its life-cycle, and, if this is so, it may explain the distribution of the species. Unfortunately, nymphs of this species are difficult to obtain in anything but small numbers, and it has not been possible to obtain any numerical confirmation of the above supposition. If it is true, however, it seems most likely that the species takes two years, because the closely allied species *C. torrentium* grows to its full size in one year, and the full-grown nymph is nearly as large as that of

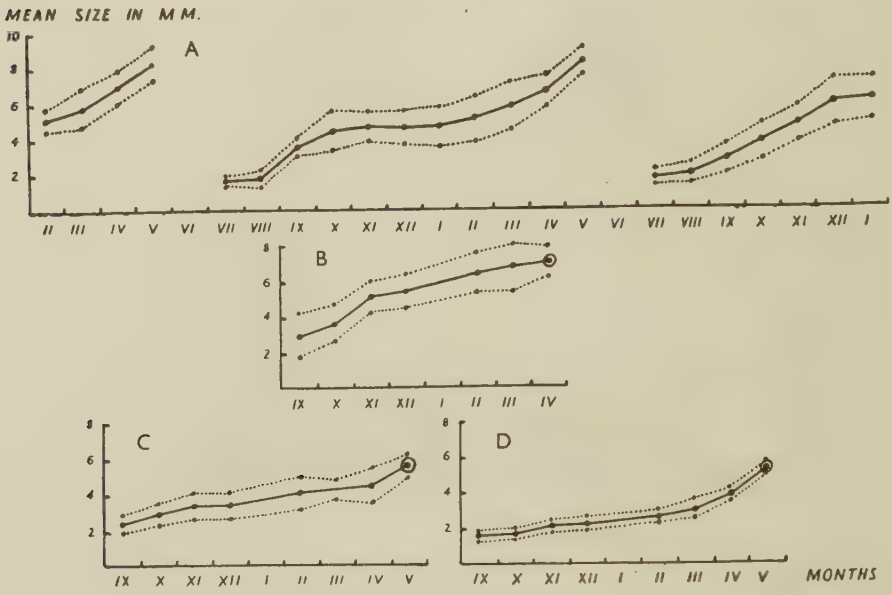

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Fig. 21.—Graphs showing the mean growth over several months in chosen localities of the nymphs of three species. The mean size, and on each side of it the standard deviation from the mean (dotted lines), is plotted against the months in which the samples were taken.

A, *Protonemura meyeri*, WI, R. Liffey, Ballysmuttan, ii.1929–i.1931, 3533 specimens (*W. E. Frost*); B, *Pr. meyeri*, WL, R. Rothay, ix.1939–iv.1940, 415 specimens (*Hynes*); C, *Chloroperla torrentium*, WL, R. Rothay, ix.1939–v.1940, 577 specimens (*Hynes*); D, *Amphinemura cinerea*, WL, R. Rothay, ix.1939–v.1940, 1918 specimens (*Hynes*).

Where the mean size is surrounded by a circle, adults were found when the nymphs were collected.

C. tripunctata. The young nymphs of the two species of this genus are most easily separated on the difference in size which they display during the summer months (p. 491). *C. tripunctata* is usually 3 to 4 mm. long before the first specimens of *C. torrentium* emerge from the egg in June.

The growth rate of stonefly nymphs has not before been made the object of special study, although Schoenemund (1925b) reared *Perla cephalotes* in captivity and has given measurements at different ages, and Wu (1923) has shown that in some American species of *Nemoura* growth continues steadily throughout the life of nymphs kept in field cages. Little is known about the various instars of stoneflies. Wu records 22 in his *Nemoura*, and Schoenemund,

33 in the females and fewer in the males of *P. cephalotes*. Samal (1925) records 22 in *Perla abdominalis* Burm. As Samal points out, the number of cercal joints increases with age, and might form a means of separating instars.

The growth rate of many species in the Lake District was investigated, collections being made from chosen localities at approximately monthly intervals from September 1939 to August 1940. Care was taken when making these collections to see that every specimen caught was taken, each was then measured and all were placed into $\frac{1}{4}$-mm. frequency classes. From this, the mean size of the population for each sample was calculated, and a curve showing the mean growth was obtained. Some of these curves are given here (fig. 21 B, C, and D), and with them is plotted the standard deviation from the means to give some indication of the scatter around each mean. From these it can be seen that the mean growth is fairly steady, and is not much affected by the cold of the winter months. Similar curves were obtained for all species investigated, although for many species rather few specimens were obtained during some collections and the mean size varies considerably. In 1929 and 1930 Miss Frost made similar collections of some species in Ireland while working on the River Liffey, and her figures for *Protonemura meyeri*, which she has kindly allowed me to use (fig. 21A), show a much greater retardation of the mean growth in the winter months than was found in the Lake District in the River Rothay. The reason for this is not clear, because the winter of 1939–40, when the observations on the River Rothay were made, was particularly severe, and one would have expected it to have had a greater effect in slowing down the growth than the normal winter of 1929–30.

Growth of the very small nymphs could not be investigated in the field, because specimens below about 2 mm. are extremely difficult to find, but it seems that it is slow. This is illustrated well by *Leuctra fusciventris* and *L. geniculata* (fig. 22 E and F), which both emerge in the late summer and autumn, but whose nymphs remain too small to find until March or April. It might be supposed that the incubation period of the egg is very long, but that this is not so, for at least some species, has been shown by hatching the eggs in the laboratory (p. 553).

Fig. 22, showing the growth rate in the Lake District of the six British species of the genus *Leuctra*, is given, although some of the collections on which the mean sizes of *L. moselyi* and *L. geniculata* are based are small, because it shows the sizes of the species during the various months of the year, and these are important for identification of the nymphs (p. 500). The curves for *L. hippopus* and *L. nigra* are based on large collections of nymphs, and can be regarded as giving a reliable indication of the mean growth. For nearly all points in all six of these curves, the standard deviation from the mean sizes is less than 1 mm., so that about 95% of the population of each species lies within the band 2 mm. above and below each curve.

From these observations, it may be concluded that in the Lake District the growth rate of the nymphs of stoneflies is not greatly affected by the cold of the winter months, although, at least in *P. meyeri*, it may be retarded during the winter in other parts of Britain.

A point of interest is the great difference in growth rate between *P. mortoni* and *Perla*. *P. mortoni* attains its full size of about 25 mm. in one year, while *P. carlukiana* (fig. 20B) grows to a mean size of only 1·9 mm. in the first year, and 9·72 mm. in two years, taking three years to reach a mean size of 24·17 mm. Both species show similar feeding habits (p. 533), and occur in the same bodies of water. Similarly *D. bicaudata* makes much more growth in one year than

either species of *Perla*, and all the smaller species are larger when full grown than are one-year-old specimens of *Perla*. This difference in the amount of growth in one year is too great to be accounted for entirely by the long incubation period of *Perla* (p. 551).

It was observed that in the small stony streams the species *Isoperla grammatica* grew more quickly than in the rivers, and accordingly parallel samples of this species were taken from a small stream (Boathouse 2 Beck) and a river (R. Rothay), both of which flow into the north end of Windermere. The mean growth in each was found to be similar to that found in other species in that there was no marked retardation in the winter, but the growth rate in the two

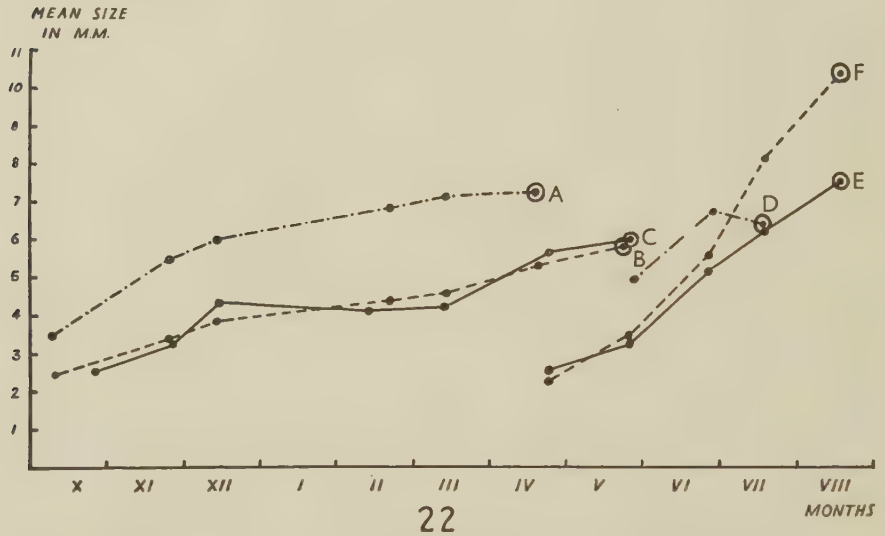

Fig. 22.—Graphs showing the mean growths between x.1939 and viii.1940 in chosen localities in the Lake District of the six British species of *Leuctra*. A band 2 mm. on each side of each mean size includes about 95% of the population.

A, *L. hippopus*, Wray, Boathouse 2 Beck, 470 specimens; B, *L. nigra*, Wray, Boathouse 2 Beck, 1618 specimens; C, *L. inermis*, R. Rothay, 232 specimens; D, *L. moselyi*, Wray, Belle Grange Beck, 43 specimens; E, *L. fusciventris*, R. Rothay, 414 specimens; F, *L. geniculata*, R. Rothay, 58 specimens.

Where the mean size is surrounded by a circle adults were found when the nymphs were collected.

localities was seen to be very different. In order to test the significance of this difference, the straight line which would best fit the data from each of the localities was calculated, and it was then possible to determine the standard error of the difference between the two linear regression coefficients of length on time. Straight lines were fitted to the data because, as explained above, the growth rate was more or less uniform throughout the period during which samples were taken. The values of the regression coefficients were 0·74772 for the stream, and 0·61185 for the river, and the standard error of zero difference is 0·039, or less than a quarter as much as the observed difference between them, showing odds of about 999 to 1 against so great a difference being due to chance. The difference in mean growth rate is therefore highly significant. The two straight lines and their relationship to the mean sizes during the different

months are shown in fig. 23. This great difference in mean growth rate between two types of locality was not observed in other species, and is possibly correlated with the different feeding habits of this species observed in the two habitats (p. 534), which in turn may be due to the availability of the different foodstuffs,

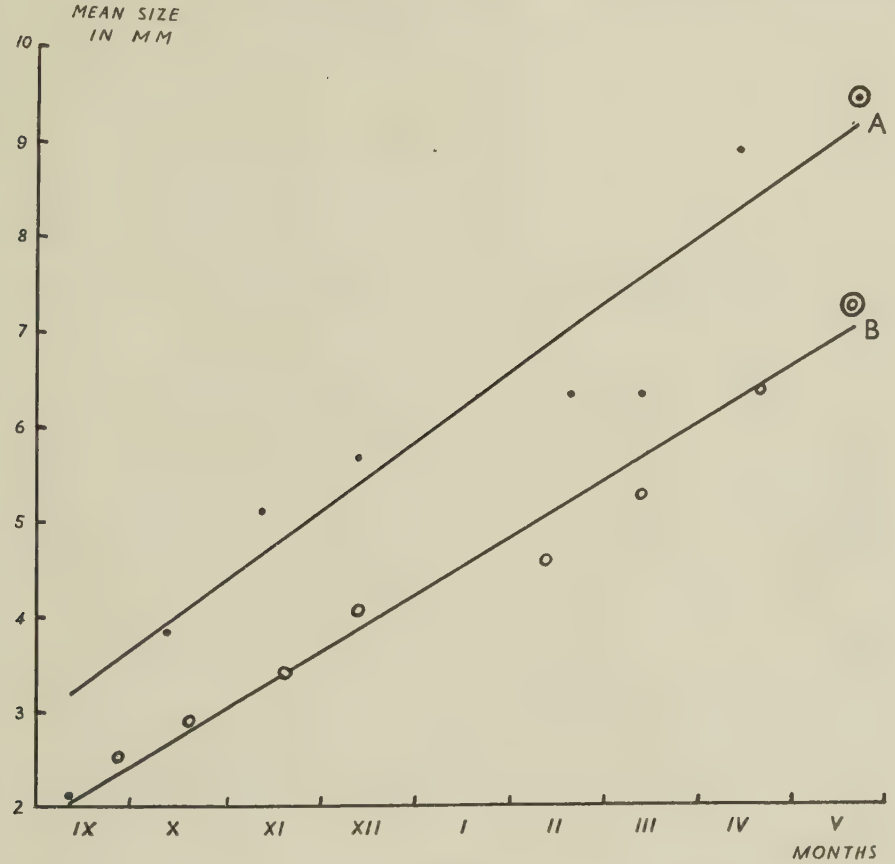

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FIG. 23.—Graphs showing the mean growth rate of *Isoperla grammatica* between ix.1939 and v.1940 in : A, A small stony stream (WL, Wray, Boathouse 2 Beck); B, A stony river (WL, R. Rothay).

The mean sizes of the samples from each locality are shown as spots for A and small circles for B, and the straight line showing the growth rate which best fits the data is drawn for each locality. Where the mean size is surrounded by a circle adults were found when the nymphs were collected.

animals being more abundant in small streams than in rivers, because the current is less strong and does not sweep away the dead vegetable matter on which many of them feed.

5. Discussion.

Schoenemund (1924 and 1925b) has stated that industrial pollution of bodies of fresh water exterminates the stonefly fauna and has indicated that the occurrence of some species in certain bodies of water is influenced by the

oxygen content, the substratum, and the rate of flow of the water. Kühtreiber (1934) and Mertens (1923) have described in general terms the habitats of various species and genera, but no real attempt has been made to define the factors controlling the distribution of stonefly nymphs, or the effect which the environment may be supposed to have on them.

From the data given in the previous sections it appears that, at least within the Lake District, five major factors control the distribution of stonefly nymphs in the various types of habitat. These are :—

(1) *The movement of the water.*
(2) *The altitude*, which is probably a function of temperature.
(3) *The substratum*, which is to a certain extent controlled by the movement of the water.
(4) *Drought* and its relation to the length of nymphal life of the species and the emergence period of the adults.
(5) The proximity of habitats in which stoneflies are abundant; this factor may be called *colonisation.*

Although these five factors are discussed separately below it must be pointed out that the first four are closely related. The movement of the water controls the substratum to a certain extent, because it controls deposition of silt and similar matter. The altitude affects the drying up of streams, because at high altitudes the rainfall is higher than at low altitudes; and this, coupled with the boggy ground found in many high places, which releases the water slowly, prevents the high streams from drying up completely. Similarly the amount of water movement and the altitude are closely related with regard to the oxygen content of the water. The amount of water movement directly affects the amount of dissolved oxygen, but this is also affected by temperature, cold water being able to take up more oxygen than warm water. Temperature is itself affected by altitude, high bodies of water being colder than similar bodies at low altitude. It can therefore be seen that the oxygen content in high bodies of water is higher than that in similar bodies of water at low altitudes. This effect of temperature on oxygen content may be the mechanism by which the upper limit threshold temperatures mentioned below come into operation. It has not, however, been possible to confirm this because no chemical analyses have been made.

(1) *The movement of the water.*

This is the most important factor in that it controls the oxygen supply, the food, and, to a considerable extent, the substratum. Stoneflies are very rarely found in completely stagnant water, but two species occur in almost every other type of still water. As, however, most of the species are confined to shallow running water or wave-washed shores, it seems that, as Schoenemund has pointed out, the oxygen content of the water is important in controlling their distribution. Stony lake shores, although still water in the strict sense, are comparable with running water in that wave action causes oxygenation, and produces the effect of a current on the substratum. The movement of the water also affects the vegetation, and the deposition of dead terrestrial vegetable matter and detritus, which form directly or indirectly the food of many stonefly nymphs. It will be seen from fig. 19 that many species are confined to running water, and this is probably due to the need for high concentrations of oxygen such as are found there. Other species occur both in running water and on stony lake shores, and these probably have a lower oxygen threshold than those

which are confined to running water, because during still weather no waves are produced, and the oxygen content of the water must fall considerably. *Nemoura variegata* and *Nemurella inconspicua*, unlike most species, occur in still or gently flowing water, and, because of this ability to withstand low concentrations of oxygen, are found in many types of locality. It is not possible, however, on the basis of the oxygen content of the water, to explain why *Capnia nigra* occurs on stony lake shores and not in running water, but this may be an effect of temperature and is discussed below.

On stony lake shores, apart from oxygenation of the water, the amount of water movement is of importance in other ways. On exposed shores, where the wave action is often extremely violent, the deposition of detritus, silt, and dead leaves is prevented, and no rooted vegetation can grow. Consequently the smaller species, such as *Nemoura avicularis* and *C. nigra*, are unable to find food and shelter, and are eliminated. The large nymphs of *Dictyopterygella bicaudata*, however, find sufficient shelter under the large stones, and feed on animals such as Ephemeroptera, which are able to live in exposed situations. Similarly, it appears that the slender nymphs of *Leuctra fusciventris* are able to work their way down into the gravel and find there sufficient higher plant tissue and detritus on which to feed. On more sheltered shores wave action does not prevent the deposition of detritus, dead leaves, silt, and sand, and small-rooted plants such as *Littorella*, *Isoetes*, and *Lobelia* appear. On these shores *C. nigra* and *N. avicularis* are common, and *Leuctra nigra*, which in running water is always found in silty pools, may also be present. Small specimens of *D. bicaudata* are also often present, but it seems that the well-grown nymphs cannot find crevices under the stones which are large enough to contain them, because of the silt, and they are therefore much less common here than on the exposed shores.

In running water the rate of flow is similarly important. In sluggish rivers and streams emergent vegetation can develop, and this forms a still-water habitat in which *N. variegata* and *N. inconspicua* can live; similar habitats develop in the most sheltered parts of stony lake shores Also, when the current is slow, rooted vegetation develops on the mud which is deposited, and here *N. avicularis* and *Taeniopteryx nebulosa* occur. It can be seen that the physiographical conditions in such vegetation are similar to those on a sheltered stony lake shore, in that the current is not strong, and there is much vegetable matter present. The reason why *N. avicularis* alone among the lake-shore species is present in such situations is probably that its long legs enable it to walk about the vegetation. It is noticeable in this connection that the four species which are normally found on rooted vegetation, namely *T. nebulosa*, *N. avicularis*, *N. variegata*, and *N. inconspicua*, are all species with particularly long legs. Fast-flowing water is usually shallow and has a stony substratum without rooted vegetation, and here the rate of flow is important because it controls the deposition of dead leaves and detritus. As some species are dependent on these as foodstuffs, they are eliminated where the current is strong, as in the stony rivers. Such species are *Protonemura praecox* and *Nemoura cambrica*. Species of the genus *Leuctra* might, from their feeding habits, be supposed to be similarly eliminated from the stony rivers, but the nymphs of *L. hippopus*, *L. inermis* and *L. fusciventris* are able to live in rapid currents. This is because the slender nymphs of these species are able to work their way down among the stones and gravel, and to find there such vegetable matter as is deposited. The same applies to the slender nymphs of *Chloroperla*, which are to a certain extent dependent on such matter for food. Usually, however,

these slender nymphs are more abundant in the smaller streams, where they find a more abundant food-supply. The stout nymphs of the NEMOURIDAE are, however, unable to burrow into the gravel, and probably for this reason they are absent from the stony rivers. *Amphinemura cinerea* and *Protonemura meyeri* are exceptions, the former probably because its small size enables it to burrow like *Leuctra*, and the latter because in the rivers it lives in the moss on the tops of stones, where it finds food and shelter. In this connection it is interesting to note that the nymphs of the large species *Leuctra geniculata*, which are confined to large streams and rivers, adopt a completely burrowing habit when they have grown to a certain size, and it is remarkable that this size is about that of the full-grown nymphs of the previously mentioned three species of the genus. *L. nigra* is not found in the rivers, probably because it is dependent on the large quantities of silt among which it is always found. Species dependent on animals and algae as food, such as *Perlodes mortoni*, *Perla* spp., and *Isoperla grammatica* are not similarly affected by the current, because algae grow well in strong currents, and on them feed many animals which form part of the food of these nymphs. So, as long as the nymphs of these species are able to prevent themselves from being swept away, the current does not affect them.

(2) *The altitude.*

Many species have been found not to occur above a certain altitude, and one, *D. bicaudata*, has been found in running water only above 700–1000 ft., but it also occurs in lakes down to about 100 ft. This suggests that, at least in this one species, the effect of altitude is one of temperature, because it is to be expected that a large body of water at a low altitude will show less rise of temperature during the summer than small streams at similar altitudes, and is, therefore, comparable in this respect with a high stream. It appears from this that *D. bicaudata* has a threshold temperature above which it cannot exist, and that this temperature is reached in the low streams during the summer. Schoenemund and Mertens mention that it is always found in very cold water, and Kühtreiber (1934) suggests from its distribution in Europe that it is a boreo-alpine species. This is borne out by its distribution in the Lake District. In the streams below 700–1000 ft., the lower limit of *D. bicaudata*, the nymphs of *P. mortoni* occur, and the two species were never found together. It seems therefore that *P. mortoni* is also affected by temperature, but by a lower limit, instead of an upper limit, threshold. *P. mortoni* is absent from the stony lake shores, but this may be due to a lower oxygen content, due to less movement of the water, and not to temperature; it is, however, interesting to note that these two closely allied species are both common in the Lake District but are never found together. Dodds and Hisaw (1925) have shown a similar altitudinal zonation of some species in America.

It is probable that similar lower limit threshold temperatures exist for all the species which are not found right up to the sources of the streams at 2000 ft. and, if so, it is to be expected that the altitude at which these temperatures are reached will vary with the latitude. A similar effect of temperature may explain the distribution of *C. nigra* in the Lake District. If it is supposed that this species, even more than *D. bicaudata*, is unable to withstand high temperatures, it could not occur in small bodies of water unless these were at a very high altitude. And even if this altitude is less than that of the sources of the high streams in the Lake District, it might be too high for there to be a sufficient area of water above it to allow the species to maintain itself. Adults

of *C. nigra* have, however, been recorded from running water in many parts of Britain, and it seems unlikely that the temperature of these is less throughout the year than that of the high streams in the Lake District.

(3) *The substratum.*

This affects the distribution of the species within the bodies of water, and it also has some influence on their general distribution. The effect of this factor on stony lake shores and its relation to wave action have already been discussed, but it must be pointed out that while the physiography of these shores is largely controlled by wave action, this is itself dependent on local geography. As Moon (1934) has shown, exposed lake shores occur where there is an outcrop of rock, which remains as a promontory projecting into the lake, and is therefore much more wave-beaten than the softer more eroded portions of the shore. Similarly, while the current of running water can influence the substratum by the deposition of silt and similar material, it cannot affect large stones and boulders, which, being fixed, form a different type of substratum from the shifting smaller stones and gravel. These two types of substratum, which in most bodies of running water are clearly defined, have been referred to above as stable and unstable substrata. On stable substrata moss, usually *Fontinalis* and *Hypnum*, develops on the tops of the stones, and forms different micro-habitats from those found among the stones and gravel. On stable substrata *Perla cephalotes* is more common than *P. carlukiana*, and this may be due to the difference in colour between the nymphs of the two species. *P. cephalotes* is dark, and is almost invisible against the dark-coloured lichens and moss which grow on stable substrata, and *P. carlukiana*, which is black and yellow, is obvious in such localities, but difficult to see against the light-coloured stones and gravel of unstable substrata. The small slender species, such as *Chloroperla* spp. and *Leuctra* spp., are almost absent from stable substrata, presumably because they are not adapted for clinging on to moss, but stouter nymphs such as *I. grammatica* and *A. cinerea* which have long legs occur on either type of substratum. *L. geniculata*, which lives down in the substratum, is, as would be expected from the above considerations, unaffected by its stability, although it is more difficult to find in stable substrata, because it is less easy to dig out the stones.

(4) *Drought.*

Many of the low streams dry up regularly every year, and though this does not affect some species, others are found to be eliminated from streams where it occurs. Fig. 19 shows that species occurring regularly in such streams are *P. mortoni*, *I. grammatica*, *Brachyptera risi*, *L. nigra*, *L. hippopus*, *P. meyeri*, *P. praecox*, *N. erratica*, and *N. cambrica*, and these are all species of which the adults emerge in the spring, and have a one-year life-cycle. In the Lake District, droughts usually occur in the early summer, and the streams are therefore dry when the nymphs are very small, or before the eggs have hatched. It seems, therefore, that the very early stages can withstand drought, possibly because the young nymphs are able to work their way down into the substratum and so prevent themselves from being dried up. Older nymphs are, however, killed by drought. Evidence of this was obtained during the severe drought of 1940, when a stream which does not normally dry up was reduced to a series of pools. Nymphs of *P. carlukiana* were found dead in the dry reaches of the stream, and the population of *L. fusciventris* and *L. moselyi* was greatly reduced.

Shortly after the drought it was possible to find stonefly nymphs only near points in the stream where there had been pools. Species having a two- or three-year cycle, such as *C. tripunctata* and *Perla* spp., are therefore unable to live in streams which dry up, and the same applies to species such as *L. moselyi* and *L. fusciventris*, which emerge during the late summer and autumn, and are therefore about half grown during the dry season. *L. inermis* and *A. cinerea*, adults of which emerge in early summer, are found occasionally in streams which dry up, but only in the larger streams of this type which are dry later in the year, and allow time for the adults to emerge before they dry completely. Young nymphs of *L. fusciventris* were often found in small streams before the dry period but were absent after the drought. This species is extraordinarily abundant and the adults fly more than most stoneflies, so it is possible that the occurrence of the species in localities where it could not survive is due to colonisation, which is discussed below.

(5) *Colonisation.*

In many localities species have been found which do not occur in similar localities a short distance away, but it has always been found that the species in question was abundant in another body of water close at hand. Species in which this has been observed are *I. grammatica*, *C. torrentium*, *A. cinerea*, and *N. cambrica*, which have been found in trickles, *B. risi* and *P. praecox*, which were occasionally found in the moss in rivers, and *L. fusciventris* which was found in spring in small stony streams which dried up later in the year and exterminated the nymphs. It seems that the adults fly to the new habitat and lay their eggs, and that some nymphs grow and may reach maturity. The species do not seem, however, able to maintain themselves, particularly in trickles, although this may often be due only to the small number of specimens which these can support.

On the basis of the five factors in distribution it is possible to explain the distribution of all species except *N. erratica*. *N. erratica* was found to be common in only one small stony stream, Boathouse 2 Beck, WL, which dries up every summer. A few specimens were also taken in high streams. Boathouse 2 Beck does not differ in any obvious particulars from several small streams within a mile of it, in which the species was not found, and it seems very unlikely that there can be any chemical differences between these streams which could control the occurrence of this species.

In conclusion, it seems desirable to stress a point which has been touched upon while discussing colonisation. This is, that, in considering the fauna of small bodies of water, the size of the locality is often of great importance. Small bodies of water are often not large enough to support a sufficient number of specimens of a given species to allow it to maintain itself there, although the conditions may be ideal as far as the individual animals are concerned. This is illustrated by the absence of the larger species such as *Perla* spp., *P. mortoni*, and *I. grammatica* from trickles and many small streams in which conditions are suitable for the species, but where the space is too limited to allow many individuals to live. That individuals of such species are able to live in these habitats is shown by the occasional colonisation of them by the larger species, but this can occur only where these species are abundant in other localities close at hand.

V. Notes on the biology of the adults.

The following section consists of notes on the adults which do not fit conveniently into any other part of the paper, but which have been considered worthy of inclusion.

Schoenemund (1924) and Kühtreiber (1934) have written at length on the behaviour of adult stoneflies, and it is proposed here only to summarise their observations, where they agree with observations made in the Lake District, and to discuss two subjects in more detail; namely, the feeding habits, and the brachypterous condition found at high altitudes, neither of which has before been made the object of special study.

1. Emergence.

When the full-grown nymph is ready to emerge, it migrates to the edge of the water, and climbs out. Most specimens remain close to the water, but some, especially in the larger species, may walk several yards from the bank or climb many feet up the trunks of trees. The nymph then fixes itself firmly to the substratum by its claws, and its skin splits down the thorax and along the epicranial suture. Katheriner (1901) states that, if the nymph *Perla maxima* Scop. cannot find a place to which it can attach itself firmly by its claws, it everts its fore gut and waits till it dries and sticks on to the substratum before the adult emerges. This has not been observed in British species. The adult emerges slowly, the thorax and legs being the first parts to appear; the wings follow, and then the abdomen and cerci, when these are present. The wings expand rapidly, and are held over the back, like those of a butterfly, until they are dry; they are then folded obliquely like those of a caddis fly, and remain in this position until the cuticle begins to harden. At first the cuticle is soft and white, although in most genera there is a complex black pattern on the thorax and abdomen. One or two hours after emergence the colour darkens rapidly, and the cuticle becomes hard.

2. Behaviour.

Most species stay close to the water in which they lived as nymphs, lurking under stones, or, in the green genera *Isoperla* and *Chloroperla*, under leaves. All species run when disturbed and do not attempt to fly, but on warm sunny days specimens of all the smaller genera can be seen on the wing near the water.

The larger species have not been seen by me to fly spontaneously, with the exception of two females of *Perlodes mortoni*, but long-winged females of *Perla* can be made to fly by throwing them into the air. The flight is, however, clumsy and unsustained. All species fly slowly and in a straight line. One or two days after emergence copulation occurs, and a few days later the eggs are produced. The males seem to be attracted only to females ready to copulate, and this attraction seems to be due to some substance extruded by the female, because a male *Capnia nigra* was seen to try to copulate with a female *Leuctra nigra* which had been in contact with a ready female of *C. nigra*, even in the presence of other females of *C. nigra*. In the laboratory the adults live for only two or three weeks, and the same seems to occur in the field.

In any one locality the emergence of some species is often very sudden, and may last for only two or three weeks, after which the adults become rare. This applies especially to the species *Perlodes mortoni*, *Dictyopterygella bicaudata*, *Perla carlukiana*, *P. cephalotes*, *Leuctra inermis*, *L. moselyi*, *Protonemura praecox*,

Nemoura avicularis and *N. erratica*. Other species, among which may be mentioned *Isoperla grammatica*, *Chloroperla torrentium*, and *Leuctra fusciventris*, continue to emerge from one locality for many weeks. The dates between which these emergences occur vary with the year and with the altitude. The small species seem to emerge at any time of the day or night, but it seems that the PERLODIDAE and species of the genus *Perla* emerge only at night, because no newly emerged specimens have been found during the daytime, even under laboratory conditions.

3. Feeding habits.

The feeding habits of adult stoneflies have been discussed by several earlier workers. Schoenemund states that the mouth-parts of adult stoneflies are reduced, and that they do not feed. Kühtreiber, who noticed that in the TAENIOPTERYGIDAE, CAPNIIDAE, LEUCTRIDAE, and NEMOURIDAE the mouth-parts are not reduced, states that he cannot explain this because the adults of these families were not observed to feed. On the other hand, Newcomer (1918) describes how in California species of *Taeniopteryx* cause considerable damage to fruit trees by eating the buds. Investigations were carried out at Wray Castle on twenty-five British species, and it was found that only members of the families PERLODIDAE and PERLIDAE do not feed as adults. Specimens of several species in the other four families were collected in the field, and it was found that they had algae belonging to the Chlorococcales, and fungal filaments in their guts, and from this it was concluded that lichen had been eaten. Similar specimens were found to deposit faecal pellets, and, as it was found that the guts of ripe nymphs and newly emerged adults were always empty, it appeared that the adults must have been feeding as adults. Accordingly, adults of each of the available twenty-five species were kept in tubes for two or three days to make them hungry, and were then placed with water and a small piece of twig on which was growing lichen and algae belonging to the Chlorococcales. All species drank as soon as they found the water, but members of both sexes of all the species of the TAENIOPTERYGIDAE, CAPNIIDAE, LEUCTRIDAE, and NEMOURIDAE also chewed at the lichen and algae on the twigs, and later deposited large numbers of faecal pellets. Attempts were made to see if any of the species would feed on the buds of cherry and apple trees as described by Newcomer, but all species, including *Brachyptera risi*, merely scraped at the bark below the buds. No member of the PERLODIDAE or PERLIDAE was observed to feed or deposit faecal pellets, and no sign of food was found in the guts of any specimens examined. It seems therefore from these observations that the TAENIOPTERYGIDAE, CAPNIIDAE, LEUCTRIDAE, and NEMOURIDAE feed on lichens and small algae, while the PERLODIDAE and PERLIDAE use their mouths only for drinking. As far as could be determined by inspection of the faeces, digestion of broken cells had taken place, but many of the unbroken cells seemed to be still alive after passing through the gut.

4. Brachypterous condition at high altitudes.

Kühtreiber states that he found short-winged specimens of both sexes of *Leuctra braueri* and *L. inermis* at 2100 metres above sea-level in Austria, and the same thing has been observed at much lower altitudes in the Lake District. Specimens of the species *L. hippopus* and *L. inermis* were collected up to a height of 1800 ft. in several small stony streams at the head of Windermere, and it was found that above about 800 ft. the wings became reduced, and, although insufficient material was obtained to allow of statistical examination,

it seems that the reduction in length of wings is gradual, the wings becoming shorter as one goes up from 800 to 1400 ft. The average length of the wings of specimens of *L. hippopus* collected at 125 ft. above sea-level was, male $5\frac{1}{2}$ mm., female $6\frac{1}{2}$ mm., and of specimens collected between 1400 and 1800 ft., male $3\frac{1}{2}$ mm., female $4\frac{1}{2}$ mm. With these short-winged specimens of the two species were collected normal specimens of *Dictyopterygella bicaudata*, *Chloroperla torrentium*, *Leuctra moselyi*, *Protonemura meyeri* and *P. praecox*, and full-grown nymphs of *Nemoura cambrica* collected at 1400 ft. produced normal adults a few days later in the laboratory. A single male specimen of *Nemoura erratica* was, however, collected at 1500 ft. and was found to be distinctly brachypterous, the wings only just reaching to the tip of the abdomen, as in the short-winged specimens of *L. hippopus* and *L. inermis*. The reason for this brachyptery at high altitudes in some species and not in others is quite unknown. It does not appear to be an effect of temperature, because there is no evidence that latitude has any influence on the length of the wings of stoneflies. It may be suggested, however, that the lack of flying ability which results from reduced wings may be of some advantage to stoneflies living in open mountainous districts, in that the insects are less liable to be carried far from the streams which are essential for their existence.

VI. Eggs and oviposition.

Percival and Whitehead (1928) have described the eggs and oviposition of several species of British stoneflies, and stonefly eggs have been mentioned and described by various European workers (Imhof, 1881; Rousseau, 1921; Samal, 1923; and Kühtreiber, 1934), whose descriptions, however, do not always agree. In the course of my investigations, the eggs of several species were obtained, and some species were seen to oviposit in the field. The eggs of some species do not entirely agree with the descriptions given by Percival and Whitehead, so these have been redescribed, and where agreement with Percival and Whitehead is complete, brief descriptions have been given for comparison with other species. The process of oviposition is described where possible after the description of the egg of each species or genus.

Perlodes mortoni.

The egg (fig. 24A) was found to agree with the description given by Percival and Whitehead; it is roughly tetrahedral in shape, and has a hard dark-brown chorion. From the base of the tetrahedron, which is slightly concave, arises a conical structure, which Percival and Whitehead have termed the basal plate. When seen by reflected light this is white. Attached to the edges of this basal plate is a membrane, which completely envelops the egg, and on which are a large number of small sticky mushroom-shaped bodies, arranged in tracts opposite the edges of the underlying egg. Similar but slightly larger structures are found all round the edges of the basal plate. These bodies, which Percival and Whitehead have termed adhesive knobs, attach the egg firmly to the substratum, those on the basal plate being the most effective. Once the basal plate has become attached it can be stretched almost to breaking-point before the egg is released.

Oviposition was not observed in the field, but several females deposited their eggs in the laboratory. About three or four hundred eggs were extruded, and carried about for some hours, attached by a sticky substance all over the sub-

genital plate and on the sterna posterior to it. In each egg the membrane was stuck close to the chorion. When females came to water they swam; and in doing so wetted the eggs, which fell away one or two at a time until finally the whole mass became detached and sank to the bottom, where it disintegrated slowly. The membrane then expanded, presumably because of absorption of water into the space between the membrane and the chorion. If females

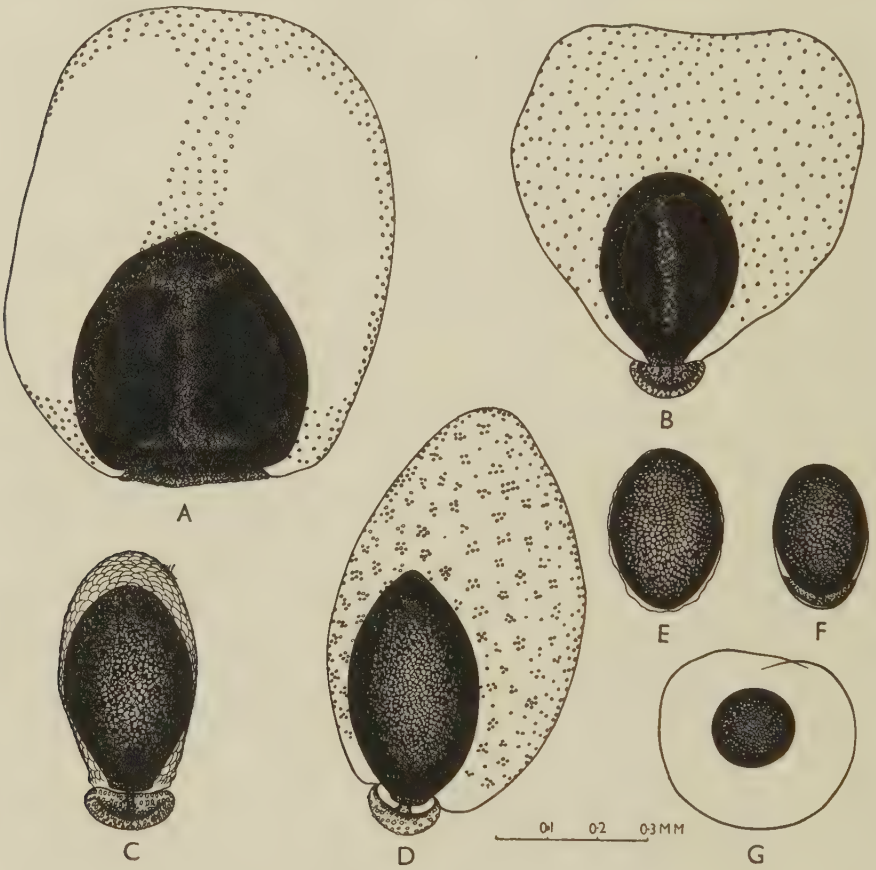

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Fig. 24.—Eggs (cl). A, *Perlodes mortoni*; B, *Dictyopterygella bicaudata*; C, *Perla cephalotes*; D, *P. carlukiana*; E, *Chloroperla torrentium*; F, *C. tripunctata*; G, *Leuctra inermis*.

were placed on water before they were ready to release the eggs, the egg mass disintegrated far less readily, and often much of it remained attached to the female. Also if females were prevented from placing their eggs in water they dropped them on the ground. Samal says that *Perla abdominalis* oviposits on the wing, and it is possible that in the field *P. mortoni* does this also, because the females can fly, although they were only twice seen to do so.

Percival and Whitehead say that the eggs took 91 days to hatch at about 15·5° C., and that the nymphs emerge through the top of the egg, which comes

off like a lid. It has not been found possible to hatch eggs of this species at Wray Castle.

Dictyopterygella bicaudata.

The egg (fig. 24B) differs somewhat from that of *P. mortoni.* The egg itself, which is light brown, is oval in lateral view, and more or less triangular in cross section. At one end it bears a small collar, from the middle of which arises a pedicel, which bears the mushroom-shaped basal plate at the tip. The basal plate is covered with adhesive knobs, similar to those found on that of *P. mortoni.* A membrane, as in *P. mortoni,* is present, but the adhesive knobs are evenly scattered all over it, instead of being arranged in tracts.

Oviposition was not observed in the field, but the females in the laboratory behaved as did those of *P. mortoni.* The wings of this species are too short to enable the females to fly, so it seems probable that similar methods of oviposition are adopted in the field and in the laboratory.

It was not found possible to hatch the eggs in the laboratory, but it seems, from observations made on the species in Windermere, that they take about two months to hatch.

Perla (Dinocras) cephalotes.

The egg (fig. 24C) is similar to that of *D. bicaudata,* but is darker coloured, and round in cross section; a collar and pedicel to the basal plate are present. Percival and Whitehead do not mention a membrane on the egg of this species, but it is possible that they did not examine fresh material, because, in all species, the membrane disappears after the eggs have been laid for a few days, or if they are preserved in formalin or alcohol. A membrane is present, but when fully expanded it is not as large as in *P. mortoni* and *D. bicaudata* and does not bear adhesive knobs. Unlike the membrane in other species examined, it is reticulate. A large number of adhesive knobs are present on the basal plate, which is the only adhesive part of the egg.

Females were seen to oviposit in the field. The egg mass was carried exactly as in *P. mortoni,* and was released as the female swam rapidly up and slightly across the stream. Two specimens were closely observed while this was in progress, and the eggs were seen to fall separately from the mass, which itself finally became detached. As in *P. mortoni,* there seems to be a time when the egg mass is ready for laying, because if females which are not ready to oviposit are thrown on to the water, the egg mass does not disintegrate. About three or four hundred eggs are present in each egg mass, and one female produced two egg masses in the laboratory.

Eggs began to hatch after an incubation period of 97 days at about 15° C., and continued to hatch for about 15 days. The nymphs emerged from the top of the egg, which came off like a lid.

Perla carlukiana.

The egg (fig. 24D) is similar to that of *P. cephalotes* but is more pointed at the top, and has a well-developed membrane, on the entire surface of which are a large number of adhesive knobs arranged in small groups. There are fewer adhesive knobs on the basal plate than in *P. cephalotes.*

Oviposition was not observed in the field, but in the laboratory the eggs were released as the female swam rapidly over the surface of the water. This species, like *P. cephalotes,* is able to fly, but no specimens were seen to do this

spontaneously, so it seems probable that swimming across the water is the usual method of oviposition.

Eggs began to hatch after an incubation period of 96 days at about 15° C., and continued to hatch for about 15 days.

Chloroperla torrentium.

The egg (fig. 24E) is ovoid, with a light-brown brittle chorion. There is no basal plate or pedicel, and the membrane is very poorly developed, and does not expand away from the egg. When first laid the egg sticks to anything with which it comes into contact, but later it becomes detached.

Oviposition was several times observed in the field. The egg mass, which contains 15 to 40 eggs, is held on and behind the subgenital plate as in *P. mortoni*. The female, with her abdomen turned down so that the egg mass sticks out below, flies upstream, and loses height rapidly, until the egg mass comes into contact with the water, when it falls off. She then usually falls on to the water herself, because of the sudden drag of the current on her abdomen, and has to take off again; several specimens were, however, seen to recover and fly up again without having done more than come into contact with the water. As in *P. mortoni* the egg mass of a female which is not ready to oviposit will not disintegrate readily on contact with water, but that of a female caught as she is flying down to oviposit falls apart at once.

Several masses of eggs incubated in the laboratory at about 15° C. began to hatch after 28 to 61 days, the usual period being about 30 days, and each egg mass continued to hatch for about 15 days. The nymphs emerged from one end of the egg which came off like a lid.

Chloroperla tripunctata.

The egg (fig. 24F) resembles that of *C. torrentium*, but has a basal plate and pedicel. The basal plate does not seem to bear any adhesive knobs, but it adheres firmly to the substratum.

Three females were seen to oviposit in the field, behaving like those of *C. torrentium*.

Unfortunately only one egg mass of this species, containing 18 eggs, was obtained, and these failed to hatch in the laboratory.

Taeniopteryx nebulosa.

The egg is slightly ovoid, and white, and has a thin chorion. An extremely sticky membrane is present which is without adhesive knobs and adheres firmly to the substratum; Percival and Whitehead describe this membrane as a jelly coat.

Only one egg mass, containing about 200 eggs, was obtained, and the female was not seen to deposit it. The eggs hatched in 24 to 26 days after incubation at about 15° C.

Capnia nigra.

The egg is round and white, and has a membrane like that of *T. nebulosa*.

Two females extruded masses of eggs a few minutes after being captured, and about an hour later deposited them in water by dipping the tip of the abdomen; the egg mass disintegrated slowly, and the individual eggs adhered to the bottom of the vessel.

The eggs of one of these females were found to have been hatched 3 days later, and those of the other began to hatch after 17 hours at 14·5° C.

Leuctra.

The eggs of three species of this genus, *L. hippopus*, *L. inermis*, and *L. moselyi*, were obtained, and were found to resemble those of *C. nigra* (fig. 24G). The membrane disintegrated a few days after the eggs were laid, but the eggs remained attached to the substratum.

Oviposition was not observed in the field, but it is probable that the process is similar to that of *Chloroperla*, because several females with egg masses were seen on the wing. About 100 eggs were present in each egg mass.

The eggs of *L. inermis* began to hatch after 28 days at about 15° C., and continued to hatch for 20 days.

Nemouridae.

The eggs of *Protonemura praecox*, *Nemoura erratica*, and *N. avicularis* were obtained, and were found to resemble those of *Leuctra*.

Females of *N. avicularis* were seen to oviposit in the field, the process being the same as that of *Chloroperla*. About 100 eggs were present in each egg mass. The egg masses of females of all three species ready to oviposit were placed in water in the laboratory, and found to disintegrate almost explosively, the eggs rushing violently apart on the surface film and then sinking. This reaction was so violent that the eggs were evenly distributed over the bottom of a 3-inch Petri dish in which the water was only $\frac{1}{8}$th in. deep; and one female *P. praecox*, which fell on the water with her egg mass, was spun round and round as the eggs flew apart. The egg masses of females which were not ready to oviposit disintegrated slowly on coming into contact with water.

Eggs of *Pr. praecox* took 18 days to hatch at a temperature of about 15° C., and those of *N. erratica* 17 to 23 days.

From these observations an interesting fact that emerges is the absence of a basal plate from the egg of *Chloroperla torrentium*, while this structure is present in *C. tripunctata*. These two species are extremely similar in general appearance, and can be reliably separated only on the genitalia. There is, however, some indication of differences in the life-history of the two species (p. 489), although it is difficult to see how this can be correlated with differences in the structure of the egg.

Summary.

Methods used for rearing stoneflies are explained, and a simple artificial stream described.

The external anatomy of the nymph is described, and descriptions of twenty-five species are made from British material. Notes from published descriptions of other species are appended, but reasons are given for the rejection of several characters used by previous workers. Keys to genera, and where possible to species, are given for specimens above 1 or 2 mm. long.

Stonefly habits are classified and those of twenty-five species are described. The feeding habits of twenty-four species were investigated, and the Filipalpia are shown to eat vegetable matter, primarily dead leaves, while the Setipalpia eat animals and algae. No entirely carnivorous species were found. *Perla*

spp. are shown to take three years to develop, while all other species investigated, with the possible exception of *Chloroperla tripunctata*, take one year. The growth rate is shown to be almost unaffected by the winter.

Movement of the water, altitude, the substratum, drought, and the proximity of other stonefly habitats are suggested to be major factors controlling stoneflies, and it is shown how these may be supposed to affect the oxygen content of the water, the availability of food, and the temperature. On this basis is explained the distribution of all species investigated, with the exception of *Nemoura erratica*, and possibly *Capnia nigra*.

The emergence and general behaviour of the adults are described, and the Filipalpia, contrary to the general belief, are shown to feed as adults, the food being lichen. Adult Setipalpia apparently do not feed. The fact that several normally winged species have been found to be brachypterous at high altitudes is discussed, but no satisfactory explanation of this phenomenon is produced.

The eggs and oviposition of fourteen species are described in varying detail.

References.

No references are given to original descriptions of adults, but papers are listed with the aid of which it is possible to identify all the British species. It has not been possible to obtain copies of a few papers, and these are marked with an asterisk.

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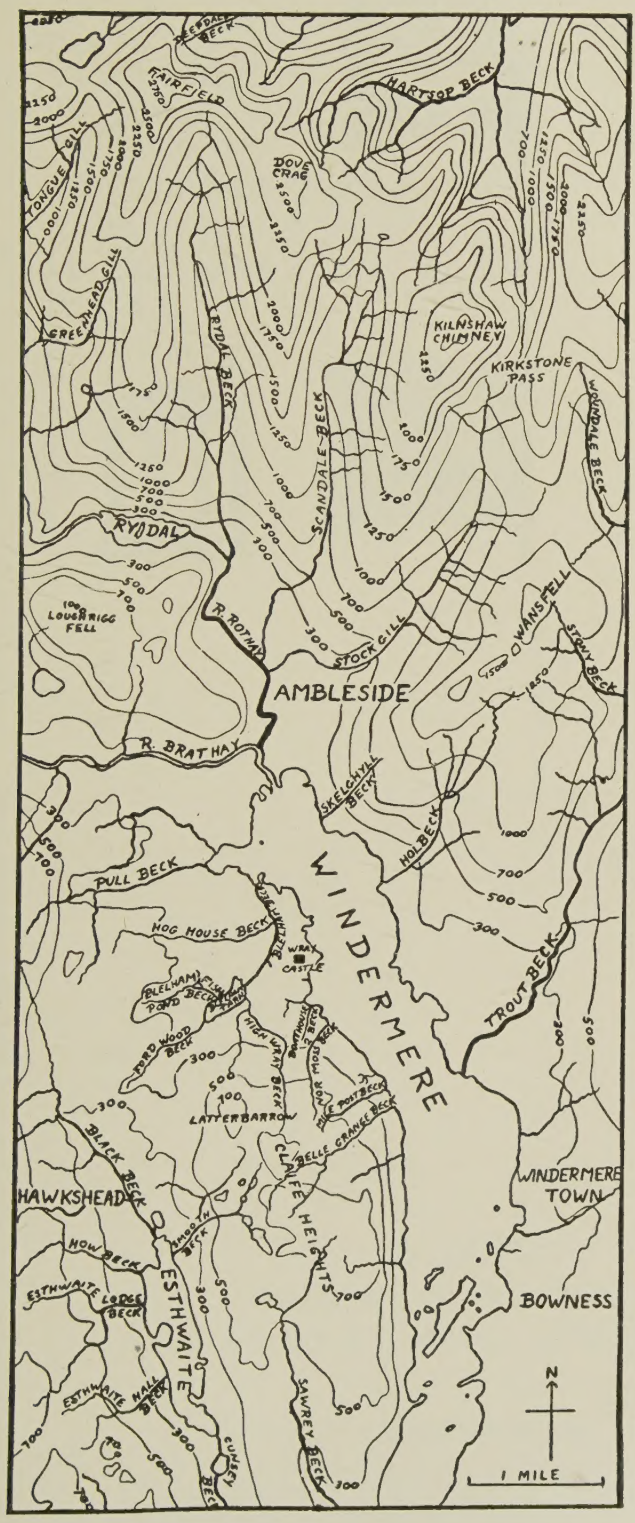

Map of the area within which most of the collections were made, showing bodies of water, contours, and towns. The names of the small streams, etc., which do not appear on the six-inch Ordnance Survey maps, are those used by the scientific staff of the Freshwater Biological Association at Wray Castle. Sign Post Trickle, the locality from which the nymphal syntype of *Nemurella inconspicua* was collected, is about 300 yards south of Wray Castle.